The behavioural ecology and predator-prey interactions of leopards (Panthera pardus) and chacma baboons (Papio ursinus) in an Afromontane environment

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Abstract

The interactions between predators and prey have long been considered to play an important role in behaviour, physiology, and evolution. Both predators and prey can influence one another's spatial and temporal patterns in activity and space use. To understand such dynamic processes, one must simultaneously assess the behavioural ecology of both predator and prey within the same environment. Such analyses have been rare in primatology.

With the aid of behavioural, telemetry, and environmental data collected between the years 2012 and 2017, a combination of methods including home range analyses, resource selection functions, activity pattern analyses and spatial regression models were used to independently test hypotheses relating to space use and activity patterns in chacma baboons (*Papio ursinus*) and their main predator, the leopard (*Panthera pardus*) within the western Soutpansberg Mountains, South Africa. Collectively, the results allowed me to test hypotheses about how baboons spatially and behaviourally respond to the threat posed by predation. The utilisation of spatial-temporal data deriving from two sympatric species provides not only a detailed assessment on how such animals independently use their environment yet is a novel approach for understanding the complex dynamics of predator-prey interactions.

My results showed that leopards established home ranges in topographically complex and highly vegetated areas while avoiding humans and also preferentially used areas of dense vegetation. Leopards were also less active in these areas, preferentially resting in areas of cover and away from human activity. Although primarily crepuscular, leopards shifted their behaviour when in proximity to humans with an increase in nocturnal activity, with day length and weather also influencing their activity scheduling. Despite the presence of leopards on the landscape, baboons primarily avoided areas that were perceived to be risky from the threat imposed by other baboon groups rather than leopards. In contrast, the probability of encountering leopards had the biggest influence on spatial variation in vigilance. In confirmation of previous studies, risk effects exceeded the importance of food availability in determining range use, although baboons selected areas of greater food availability during winter when food was shortest suggesting that they trade off an increase in risk for foraging opportunities at these times. Despite clear seasonal constraints on behaviour in winter, however, the baboons did not appear to compensate with increased nocturnal activity at these times. This study highlights the value of integrating information on both predators and prey into studies of primate-predator interactions and suggests potential avenues for future research.

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List of Abbreviations

AIC: Akaike information criterion

CSV: Comma-separated values

DEM: Digital Elevation Model

GIS: Geographic Information System

GLMM: Generalized linear mixed model

GME: Geospatial Modelling Environment

GPS: Global Positioning System

HRT: Home Range Tools

IUCN: International Union for Conservation of Nature

LLP: Limpopo Leopard Project

MLM: Makhado Local Municipality

NASA: The National Aeronautics and Space Administration

NDVI: Normalised Difference Vegetation Index

OLI: Operational Land Imager

OLS: Ordinary Least Squares

PPP: Primate Predator Project

SAEON: South African Environmental Observation Network

SANBI: The South African National Biodiversity Institute

SDEM: Spatial durbin error model

SEM: Spatial error model

SLX: Spatial lag of X model

UNESCO: The United Nations Educational, Scientific and Cultural Organization

USGS: United States Geological Survey

UHF: Ultra High Frequency

VBR: Vhembe Biosphere Reserve

Statement of Copyright

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Dedication

For Doctor Katherine Ellison,

With absolute love and admiration, you took me in when I had little hope and you changed my life forever. I am eternally grateful.

And for Uncle Kevin.

I wish you were here for this, and there is not a day that goes by when I do not think about you. I miss and love you dearly. I know you would be proud.

"Alas," said the mouse, "the world gets smaller every day. At first it was so wide that I ran along and was happy to see walls appearing to my right and left, but these high walls converged so quickly that I'm already in the last room, and there in the corner is the trap into which I must run."

"But you've only got to run the other way," said the cat, and ate it.

- *Franz Kafka (A Little Fable, Year Unknown)*

Chapter 1: Introduction

1.1 Predator-Prey Interactions

1.1.1 Defining Predation

"Predation" in the broadest sense can be defined as an interaction between two species when one (the predator) is capable of killing and consuming a portion of the biomass of individuals that are predated on (the prey) (Abrams, 2000). While the definition of predation can shift depending on the context, and has been expanded to include seed consumption and parasitism (although, parasites may not directly or instantly kill and consume prey) (Abrams, 2000), the definition of "predation" used in this thesis is more representative of the familiar relationship found in predator-prey interactions between two different species of animals. Therefore, in this context, predation can be described as a behavioural act where a predator seeks out, kills, and consumes another animal (Briers, 2006) whereas a prey item can be considered an animal species that is actively hunted and adapts behavioural strategies to avoid being predated on (Briers, 2006).

1.1.2 Predator Hunting Modes

Predators have evolved several different strategies to acquire prey. While these hunting modes can be found in nearly all predatory taxa, in this thesis, I will primarily address adaptations utilised by large predatory mammals. Broadly speaking, predator hunting modes can be defined into three categories (Mclaughlin, 1989; Miller, Ament and Schmitz, 2014).

1. Sit and wait/ambush predators: predators that remain motionless and only attack a prey item after it has moved within catching distance (e.g. polar bears, *Ursus maritimus* (Smith, 1980; Togunov, Derocher and Lunn, 2017)*;* leopards *Panthera pardus* (Jenny and Zuberbühler, 2005)
2. Sit and pursue predators: predators that stalk their prey and may remain motionless until a prey item comes close enough for the predator to be able to quickly pursue their prey through chasing (also referred to as the

"stalk-chase-kill "technique in this thesis) ((lions, *Panthera leo* (Thaker *et al.*, 2011).

3. Active hunters (also referred to as cursorial predators): predators that actively move throughout their environment as a means to track and pursue their prey (cheetah, *Acinonyx jubatus;* African wild dogs, *Lycaon pictus* (Thaker *et al.*, 2011).

Such hunting modes are generally dependent on a combination of different factors ranging from habitat characteristics (Schmitz, Krivan and Ovadia, 2004; Schmitz, 2007), prey conditions (Pierce, Bleich and Terry Bowyer, 2000), and morphological adaptations (Figueirido and Janis, 2011) and as a result, carnivore species with different hunting modes that overlap in prey species and range may also vary in terms of how they utilise their environment (Bartnick and Van Deelen, 2013). For example, cursorial predators such as wolves (*Canis lupis*) will often prefer to hunt in open habitats where they give chase over long distances until they subdue an (often unhealthy or young) individual (MacNulty, Mech and Smith, 2007; Wikenros *et al.*, 2009; Gervasi *et al.*, 2013). In contrast, mountain lions (*Puma concolor*) heavily rely on the element of surprise to subdue and kill prey items and as a result, primarily rely on habitat characteristics such as steep terrain and heavy vegetation coverage to remain undetected (Elbroch and Wittmer, 2012; Allen, 2014; Wang, Nickel, Rutishauser, Bryce, *et al.*, 2015). While both of these predators may coexist and even compete for similar prey items, the contrasting hunting modes and habitats utilised by each species have been hypothesised to allow them to occupy separate niches in the landscape (Bartnick and Van Deelen, 2013).

Sympatric predator species that reside not only in the same community yet also share similar hunting modes may coexist through altering activity levels (Hayward and Slotow, 2009; Lucherini *et al.*, 2009; Cozzi, Broekhuis, McNutt, *et al.*, 2012), spatial segregation (Durant, 2000; Welch *et al.*, 2015) and/or reducing of dietary overlap (Barrientos and Virgós, 2006; Hayward and Kerley, 2008). This is perhaps most exemplified in Africa's large carnivore guild which can contain up to five large mammalian carnivores in

intact communities ranging from ambush (lion, leopard) and cursorial (spotted hyena, *Crocuta crocuta;* African wild dog, and cheetah) predators. For example, despite the latter three species being considered cursorial and active hunters, African wild dogs and cheetahs have notably been recorded to be more active during diurnal and crepuscular hours compared to spotted hyenas (Durant, 2000; Saleni, Gusset, Graf, Szykman, 2007; Hayward and Slotow, 2009). As hyenas have been known to steal kills and predate on both species, such niche segregation may in part allow such subordinate predators to coexist with hyenas while also avoiding encounters. Interestingly enough, large ambush predators of different body sizes may not necessarily avoid one another spatially (Karanth and Sunquist, 2000), yet may simply predate on prey species of different body sizes. This has been recorded in sympatric tigers *(Panthera tigris)* and leopards (Karanth and Sunquist, 2000) as well as pumas and jaguars (*Panthera onca*) (Taber *et al.*, 1997).

Prey have been shown to adapt to the predatory modes utilised by their predators and may therefore exhibit different anti-predator strategies depending on whether they are in danger from cursorial (often active hunters) or ambush carnivores (Schmitz, Krivan and Ovadia, 2004). As ambush predators rely on cover to successfully make a kill and are likely to hunt in specific locations ("hotspots"), prey items may often exhibit greater anti-predator behaviour (i.e. vigilance) toward such carnivores compared to cursorial predators (Lima and Bednekoff, 1999; Middleton *et al.*, 2013; Donadio and Buskirk, 2016). In contrast, while cursorial predators may potentially inhibit such responses (Laundré, Hernández and Altendorf, 2001; Wikenros *et al.*, 2009; Ghosal and Venkataraman, 2013), the large hunting range exhibited by such active predators may promote prey to identify areas of high risk throughout the landscape, and as a result, dilute such effects (Middleton *et al.*, 2013). Additionally, as cursorial predators may 'test' their prey before making a kill (and as a result, may be fully exposed to prey items) compared to ambush predators that are required to be as close as possible before the final attack, anti-predator behaviour such as vigilance may not be as necessary (Creel and Creel, 2002).

1.1.3 Defining Risk

Risk can be defined as the likelihood of encountering and being consumed by a predator over time and has been characterised by Lima and Dill (1990) through the equation:

$$P(\text{death}) = 1\text{-}e(\text{-}\alpha dT)$$

In this instance, α represents the probability of an encounter between a prey item and their predator, d signifies the chances of the prey item succumbing to death as a result of predation, and T indicates the time a prey item spends vulnerable (Lima and Dill, 1990). As the various hunting modes influence where predators are likely to occur, the probability of an encounter (α) depends on components such as habitat type and predator movement. T, can also be considered as influenced by the density of predators within an area.

Risk can be difficult to directly assess and as a result, many researchers have relied on other methods to evaluate the level of risk from predation for a prey species. For example, several studies have shown that the density of predators may directly influence prey through either increased mortality (Piersma, Koolhaas and Jukema, 2003) or by altering prey behaviour such as reduced foraging time or activity levels (Lima and Dill, 1990; Anholt and Werner, 1998).

Researchers have also evaluated risk by assessing where *and* when predators are likely to be active (Hayward and Slotow, 2009; Lucherini *et al.*, 2009; Schuette *et al.*, 2013) as well as where predators are likely to kill and consume their prey (Quinn and Cresswell 2004; Hebblewhite *et al.*, 2005; Kolowski and Holekamp 2006; Gervasi *et al.,* 2013). Studies have also assessed how prey items adjust their activity levels (such as foraging rates) in response to predation risk (Lima and Bednekoff, 1999; Sih and McCarthy, 2002; Ferrari *et al.*, 2008). While all these approaches have provided valuable insights into the complexities of predator-prey dynamics, it should be noted that such a system is inherently complex and that the methods used to evaluate risk may vary between different predator and prey species as well as the environments in which they reside in.

1.1.4 Perceived Risk

Although death is often considered the ultimate cost of a predation event, *perceived* risk may also have an enduring effect on prey (Preisser, Bolnick and Benard, 2005). In such instances, the risk imposed by predators can promote several costly behaviours in prey items such as increased vigilance (Dehn *et al.,* 1990; Mooring *et al.,* 2004; Valeix *et al.,* 2009), spatial and temporal avoidance (Rettie and Messier, 2000; Thaker *et al.*, 2011; Vanak *et al.*, 2013), and increased group aggregation (Landeau and Terborgh, 1986; Creel and Winnie, 2005), which can impact long term trends in the behavioural ecology of the prey. For example, the trade-off between predator avoidance and reduced food intake can influence both a decrease in fitness and reproductive output, thereby influencing prey population levels (Lima and Dill, 1990; Lima, 1998a). Given this, these non-lethal effects can also potentially lead to local shifts in structure of ecological communities and trophic cascades (Lima, 1998a; Suraci *et al.*, 2016)

Perhaps one of the most well studied concepts regarding how predators can shape the behaviour of prey, and the surrounding environment is the landscape of fear. First introduced by Laundré (*et al.,* 2001), the landscape of fear was presented as a visual model to explain how foraging patterns and space use in ungulates was influenced by the risk imposed by newly introduced wolves in Yellowstone National Park (USA). As such, the landscape of fear can be defined as a visual representation of an animal's perceived risk throughout the landscape (Kohl *et al.*, 2018). Since then, the landscape of fear concept has been applied to explain the behaviour in a range of taxa including birds (Rösner *et al.*, 2014), reptiles (Hammerschlag *et al.*, 2015) and numerous mammalian species (Laundré, Hernández and Altendorf, 2001; Berger, 2007; van der Merwe and Brown, 2008).

Although prey items respond to the risk imposed by predation by altering their antipredator behaviour through spatial avoidance or increased vigilance, the landscape of fear extends such processes by incorporating the fear of predation to explain such patterns across time and space (Laundré, Hernández and Ripple, 2010). In this instance, fear in animals can simply be defined as an immediate

reaction to danger and the anticipation of risk (Laundré, Hernández and Ripple, 2010). Physiologically, the stress induced by fear can be measured in animals through increased heart rate or the release of glucocorticoid hormones in faeces (Clinchy, Sheriff and Zanette, 2013; Støen *et al.*, 2015). Behaviourally, fear in animals has often been found to be associated with an increase in vigilance, a reduction in feeding, and the spatial-temporal avoidance of potentially dangerous habitats (but see Beauchamp 2017 for a review on the lack of a correlation between stress hormones and vigilance).

The landscape of fear can be defined as how an animal spatially perceives and utilises its environment due to the heterogeneous risk imposed by predators (Laundré, Hernandez and Ripple, 2010). Given this, animals should be expected to forage in specific (low risk) areas, while simultaneously avoiding habitats where the risk imposed by predation increases (Hebblewhite and Merrill, 2009).

Since both predators and prey are likely to respond differently to various habitat and environmental characteristics, the landscape of fear should also be considered a dynamic and physical projection of risk. For example, Laundré and colleagues (2010) elegantly described the landscape of fear as three-dimensional, and exhibiting "peaks and valleys" that are related to predation risk, which is influenced by environmental characteristics within the habitat that can either promote or decrease the effectiveness of a hunting predator.

Three major factors within predation risk are thought to primarily influence the landscape of fear (Brown, Laundre and Gurung, 1999). The first is that a prey animal must choose where to feed while also considering the predator type that they are at risk from (Bleicher, 2017). Managing risk as a response to nocturnal ambush predators (such as felids) may therefore be considerably different compared to cursorial predators (i.e. canids, hyaenids). Secondly, perceived risk may also vary considerably depending on the hunting and consumption intensity exhibited by the predator (Bleicher, 2017). Finally, the landscape of fear may also be highly influenced by how well the focal prey species can predict the likelihood of an attack occurring (Bleicher, 2017).

In addition to the risk imposed by predation, the landscape of fear can also be heavily influenced by the availability of essential resources such as food and shelter (Laundré, Hernández and Ripple, 2010). Van der Merwe and Brown (2008) found that perceived risk in Cape ground squirrels (*Xerus inauris*) significantly decreased when in proximity to refuges such as burrows. Wirsing (*et al.,* 2007) found that dugongs (*Dugong dugon*) chose to forage in safer, yet less profitable feeding patches when faced by the risk imposed by tiger sharks (*Galeocerdo cuvier*). In contrast, animals that are physiologically or nutritionally stressed, or face seasonal variability in food or water availability, may choose to feed or drink in high risk areas, and as such, may attempt to negate potential predation opportunities by exhibiting other antipredator behavioural modifications. For example, Valeix (*et al.,* 2009) found that buffalo (*Syncerus caffer*) increased their vigilance levels rather than just spatial avoidance when attempting to access watering holes where the probability of encountering lions is high.

The landscape of fear has been found to be a powerful tool to understand the complex dynamics of how prey items spatially utilise their environment when faced with the risk imposed by predators; and ecological factors like resource acquisition and seasonality. Both direct and perceived risk are important in assessing the influence that predators have on prey behaviour, and they potentially have cascading effects on individual fitness and population level dynamics. The non-lethal effects induced by predation may also lead to trophic level shifts in ecological communities, and consequently, are a fundamental component to understanding animals and the ecosystems that they reside in.

1.1.5 The Influence of Predator-Prey Systems in Ecology

Predator-prey interactions are considered to be fundamental in shaping ecological communities (Lima, 1998a). Through trophic dynamics, apex predators can directly and indirectly influence ecosystems by consuming prey, which in turn, controls prey density (Preisser, Bolnick and Benard, 2005). Either through consuming prey or excretion, predators have been shown to mediate nutrient cycling and enhance localised ecological productivity. For example, the transportation of salmon carcasses predated by brown bears

(*Ursus arctos*) promotes the exchange of aquatic based nitrogen (*N)* into riparian forests and which has been shown to act as a nutrient rich fertiliser in such edge habitats (Helfield and Naiman, 2001; Quinn *et al.*, 2003). Furthermore, Dunham (2008) found that phosphorus (*P)* levels in soils in Tai National Park, Ivory Coast were most likely due to a trophic pathway consisting of predators (both mammalian and avian), arachnids, arthropod microbivores, and decomposing organic material.

The non-lethal perceived risk that prey items exhibit while coexisting with a predator may also have a profound impact on ecosystems (Lima, 1998b; Preisser, Bolnick and Benard, 2005; Clinchy, Sheriff and Zanette, 2013). Non-consumptive effects can manifest themselves through morphological, physical, and behavioural shifts to avoid predation and may be inherently costly and have long term consequences in shaping prey abundance and distribution (Preisser, Bolnick and Benard, 2005). Additionally, it seems likely that non-consumptive and consumptive effects may be negatively correlated, since the purpose of antipredator behaviour is to reduce direct predation (Creel and Christianson, 2008).

Optimal foraging theory suggests that animals must maximise energy intake while avoiding predation (Sih, 1980). As such, by avoiding risky habitats, prey may attempt to mediate resource acquisition while simultaneously avoiding being predated on (Lima, 1998a). Patch relocation to avoid predation may initiate trophic cascading as prey items that move to specific areas in order to reduce risk must focus consumption within that patch, consequently promoting depletion of resources as a result (Schmitz and Suttle, 2001). For example, Ford (*et al.,* 2014) found that the predation risk exhibited by leopard and African wild dog impacted where impala were more likely to feed, and subsequently influenced the distribution of *Acacia* plant communities. In this case, areas of high risk (where impala avoided) allowed for the growth of *Acacia* species that were poorly defended from consumption due to being less thorny. In contrast, areas of low risk (where impala gathered) promoted *Acacia* species that were well defended (Ford *et al.*, 2014).

Perhaps one of the most hotly debated examples of how behaviourally mediated responses can influence habitat structure comes from research deriving from

Yellowstone National Park (USA). It has been argued that patches of high risk were created as wolves began to hunt elk (*Cervus canadensis*) after their reintroduction into the park. Correspondingly, elk avoided areas where the risk of predation is seemingly high and therefore allowed the spread of woody plants such as aspen, cottonwood, and willow (Ripple *et al.*, 2001; Ripple and Beschta, 2004, 2007; Beschta *et al.*, 2016). The authors then argued that the recruitment and recovery of such riparian species was essential to the stability of river systems through stabilising eroding streambanks while simultaneously allowing for an increase in diversity of numerous songbird species as well as keystone species such as beaver (*Castor canadensis*) (Ripple and Beschta, 2012). In contrast, through the use of risk models originating from wolf winter kill sites (winter being when aspen are browsed more heavily by elk), Kauffman and colleagues (2010) found that there was no correlation between aspen recruitment and spatially mediated risk on elk by wolves. The authors conclude that this lack of a correlation may be due to a combination between the hunting style found in wolves (cursorial) as well as the fact that the antipredator responses found in elk may not be consistent enough to produce long term ecological changes (Kauffman, Brodie and Jules, 2010). As such, it may be possible that the influence that predator-prey dynamics have in ecosystems may vary considerably by habitat, predator hunting mode, and the behavioural responses exhibited by prey items.

1.2 Predation and Primates

1.2.1 Predation and Primate Evolution

Predation has long been considered to be a strong selective force that has shaped both the evolution and behavioural ecology of primates, with evidence from the fossil record clearly identifying such events as present even in large bodied hominins such as *Paranthropus robustus* (SK 54) (Lee-Thorp, Thackeray and van der Merwe, 2000) and *Australopithecus africanus* (Berger and McGraw, 2007). In extant species, there is evidence that primates ranging in size from the smallest (*Microcebus)* to the largest (*Gorilla*) have experienced mortality due to successful predation events (Hart, 2007). Although primate predators vary considerably by both study site and primate species, a meta-analysis conducted by Hart (2007) found that felids and avian predators accounted for the majority

of predation events on primate species across the globe, with the remaining predators including cursorial carnivores (canids and hyaenids), reptilians, and particularly in the case of Madagascar, small carnivores (such as the fossa, *Cryptoprocta ferox*).

The risk imposed by predation is thought to have influenced a variety of behavioural, ecological, and morphological adaptations in primates. For example, group living has been hypothesised to alleviate the risk imposed by predation by reducing the probability for any individual being consumed ('the dilution effect') (Turner and Pitcher, 1986; Dehn, Ecology and Dehn, 1990), cumulative vigilance ('the many eyes effect') (Powell, 1974), as well as the potential for groups to retaliate through mobbing (Isbell, 1994; Stanford, 2002). Predation may also have the potential to influence group composition. For example, a meta-analysis conducted by Hill and Lee (1998) found a positive correlation not only between the risk of predation and overall group size, but also the number of males within a group. Although group living may provide several key advantages for survival (such as protection from predators) it also seems likely that sociality may have the potential to impose constraints such as reproductive and resource competition.

Some primates may have evolved specific morphological adaptations to counter the risk imposed by predation including increased canine size in males and larger body size (Leutenegger and Kelly, 1977). Cheney and Wrangham (1987) found that primate species with a larger body size (excluding apes) were less likely to be predated on compared to smaller species. Despite this, larger species such as chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*) have been found to be susceptible to predation thus suggesting that a large body size alone does not completely negate risk. This is exemplified by research conducted by Zuberbühler and Jenny (2002) on predation rates of numerous primate species by leopards residing in Taï National Park, Ivory Coast, where leopards were more likely to predate on larger and more abundant primate species rather than smaller ones. The authors suggested that these contrasting findings likely resulted from how smaller species may be able to easily escape leopards by being more agile and so having the ability to escape into the canopy

during an attempted predation event. Despite this, it should also be noted that although a smaller body size combined with a more arboreal lifestyle may be effective against larger and terrestrial predators (such as felids), it may not necessarily have as much of an impact on the risk imposed by avian predators such as raptors.

1.2.2 Behavioural Responses of Primates from Predation

As an increase in group nor body size may not directly prevent predation risk from all predators, primates, like other animals, have developed an array of behavioural responses in response to the risk imposed by predators.

1.2.3 Vigilance

One of the most widespread antipredator strategies studied in primates involves vigilance, or, the act of looking (Allan and Hill 2018). Nevertheless there has been a lack of consistency regarding the actual definition and function of vigilance across studies (reviewed in Allan and Hill 2018) For example, some authors have defined vigilance as being actively wary of a potential threat (Boinski *et al.*, 2003; Smith, Kelez and Buchanan-Smith, 2004), while for others the act of scanning or gazing (regardless of the presence of a threat or not) has been used to define vigilance (Treves, 1998, 1999; Treves and Naughton-Treves, 1999; Allan and Hill, 2018). In this instance, the act of looking is assumed to serve several functions outside of just predator detection including visually searching for food, neighbours, or mates (Allan and Hill, 2018). This definition does not necessarily assume the exact behavioural state of the animal, and it acknowledges that an animal that *is* looking throughout their surroundings may be equally likely to detect threat as an animal that is cautiously alert.

One assumption in vigilance studies is that an animal must trade off foraging as a means to enhance vigilance (Metcalfe and Furness, 1984; Brown, 1999) such as in eastern grey kangaroos (*Macropus giganteus*) (Favreau *et al.*, 2014), impala (*Aepyceros melampus*) (Blanchard and Fritz, 2007), and grey squirrels (*Sciurus carolinensis*) (Bachman, 1993). Although this may be the case in other taxa, it should be noted that many primate species can feed upright, and continuously scan their environment while eating and therefore, reduce such

potential costs required to continuously scan (Cowlishaw, Michael J Lawes, *et al.*, 2004). This ability to scan and forage simultaneously can potentially allow baboons to eat while avoiding a decrease in the efficiency to scan.

As group size (and group living in general) is often considered to be an adaptation to negate the risk imposed by predation, several studies have assessed whether vigilance is influenced by the number of members found within a group. Results have varied considerably, with some researchers finding group size to either have a positive, negative, or null effect on vigilance levels (see Allan and Hill 2018). Vigilance levels have also been assessed in relation to the number of (Cowlishaw, 1998; Busia, Schaffner and Aureli, 2016) and distance to nearest neighbours (Robinson, 1981) as well as other factors including sex (De Ruiter, 1986), social rank (Alberts, 1994), and affiliation (Dunbar, 1983).

Several studies have also found vigilance levels in primates to vary spatially. In relation to lower canopy height (that is, closer to the ground while in trees), an increase in vigilance has been uncovered in ursine colobus monkeys (*Colobus vellerosus*) (Teichroeb and Sicotte, 2012), chimpanzees (Kutsukake, 2006), and brown capuchin monkeys (*Cebus apella*) (Hirsch 2002). Such an increase in relation to vertical position has often been theorised to relate to the perceived threat induced by terrestrial predators. Spatial variation in vigilance has also been linked to factors such as a decrease in visibility due to increased foliage density (Cords, 1990; Cowlishaw, 1998), and perceived risk from predation (Coleman, 2013; Campos and Fedigan, 2014). Campos and Fedigan (2014) found that white faced capuchins were more likely to increase visual scanning in areas where previous encounters with predators were more likely to occur. Furthermore, spatial variability in vigilance is not only limited to perceived risk in predation since it has also been found in relation to range overlap with other groups (MacIntosh and Sicotte, 2009) as well on the boundaries of home ranges, where such encounters are more likely to have occurred (Busia, Schaffner and Aureli, 2016). In the latter instance, it may also be likely that such an increase in vigilance may be due to the threat imposed by other groups, and the fact that the peripheries of home ranges were less familiar.

1.2.4 Vocalisations

Vocalisations have long been considered to play a prominent role in warning other group members of the immediate threat imposed by predators (Struhsaker, 1967). Despite the immediate benefit that vocalisations have in terms of warning group members of the presence of dangers, such a behaviour is considered energetically costly, and furthermore, it can lead to an increase in risk to the animal eliciting the alarm call. In such instances, the individual that elicits the alarm call is likely to be most at risk due to driving the attention of the predator to itself (Stanford, 2002). Given the costly nature of alarm calls, there are three primary theories regarding the evolution of such an antipredator strategy despite the obvious risks imposed by the signalling animal (Zuberbühler, Jenny and Bshary, 1999). First, as alarm calls often initiate responses such as flight in conspecifics, the caller may have a direct advantage by being able to strategically position itself during the chaos to avoid being caught (Charnov and Krebs, 1975). Second, eliciting an alarm call can be indirectly beneficial by enhancing the survivability of close relatives (Smith, 1965). Third, the caller can indirectly benefit by transmitting predator specific knowledge to their offspring (Curio, 1978).

In addition to warning conspecifics of the impending threat imposed by a predator, alarm calls may also alert the predator that they have been detected, and as a result, prevent an attack (Zuberbühler, Jenny and Bshary, 1999). Such strategies may be particularly effective against ambush predators such as large felids, which rely on the element of surprise to attack and will often give up targeting a group or individual after being detected (Zuberbühler, Jenny and Bshary, 1999; Isbell *et al.*, 2018). Yet such strategies may not necessarily be effective against cursorial predators that are often not deterred, even after detection (Zuberbühler, Jenny and Bshary, 1999). Zuberbühler (*et al.,* 1999) found that several species of monkeys (*Colobus badius, Colobus polykomos, Cercocebus atys, Cercopithecus diana, Cercopithecus campbelli, Cercopithecus petaurista*) were far more likely to induce alarm calls when faced with leopards rather than chimpanzees. Leopards (compared to chimpanzees) were more likely to flee rather than continue pursuing their prey upon the elicitation of an alarm call. In addition, *Cäsar* (*et al.*, 2013) found that black-fronted titi monkeys

(*Callicebus nigrifrons*) exhibited higher alarm call rates when faced with model felids compared to model raptors.

There is additional evidence to support the idea that the predator deterrence function of alarm calls can directly influence felid behaviour. In a controlled experiment, Adams and Kitchen (2018) found that ocelots (*Leopardus pardalis)* were far more likely to respond to alarm calls produced by titi monkeys (*Callicebus toppini*) and saki monkeys (*Pithecia rylandsi*) compared to control calls (loud vocalisations not associated with alarm calls). Ocelots were more likely to remain stationary during control calls yet responded by moving further away during alarm vocalisations. As such, it seems apparent that the effectiveness of primate alarm calls in terms of predator deterrence, may be due to the predator itself being able to recognise that such vocalisations represent being detected.

Although alarm calls are often elicited (and recorded) during direct encounters, such vocalisations have also proven useful in assessing perceived risk in primates. Indeed, the assessment of perceived risk in primate species that have the ability to elicit predator-specific vocalisations has been particularly useful when measuring the levels of risk imposed by different predator types. By taking into account the location of predator specific alarm calls, Willems (2007) found that perceived risk in vervet monkeys (*Chlorocebus pygerythrus*) was primarily attributed to terrestrial threats such as baboons and leopards, which correspondingly influenced space use. In contrast, at the same study site, the combined utilisation of predator specific alarm calls and distribution allowed Coleman and Hill (2014) to assess perceived risk on space use in the more arboreal samango monkey (*Cercopithecus albogularis schwarzi*). Samango monkeys were less likely to venture into areas where they elicited alarm calls in response to arboreal predators such as eagles and the effects of fear exceeded those of food availability in determining habitat choice. Therefore, alarm calls not only provide researchers with a useful understanding of the immediate behavioural states of a prey item, they also have the potential to shed light into how such vocalisations relate to other behavioural decisions.

1.2.5 Spatial Avoidance

Animals must traverse the landscape to search for essential resources such as food. Many species are required to balance food acquisition while simultaneously avoiding the risk imposed by threats such as predators and competitors (Sih, 1980; Lima and Dill, 1990; Brown and Kotler, 2004). As a result, animals often have to choose to forage in high quality food patches (and thus potentially increase the risk imposed by predation) or suffer nutritional losses by feeding in relatively safer (yet not as profitable) habitats (Schmidt and Kuijper, 2015). Spatial avoidance can be impossible for species that reside in habitats that exhibit patchily distributed food sources and where the risk of predation is homogeneous across the landscape (Schmidt and Kuijper, 2015).

As mentioned in the previous section, samango and vervet monkeys have been shown to spatially avoid areas that they perceive to be risky (Willems and Hill, 2009; Coleman and Hill, 2014). In these contexts, the more arboreal samango monkeys were observed to avoid areas where the probability of encountering avian predators increased (Coleman and Hill, 2014). In contrast, the more terrestrial vervet monkeys were recorded to spatially avoid areas that exhibit heightened risk from leopards and baboons (Willems and Hill, 2009). There is also evidence that some primate groups may not use spatial avoidance as an antipredator strategy. For instance, red colobus monkeys (Stanford, 2002) were not recorded to spatially avoid areas that were considered risky due to predators being recorded as having predated there in the past. Interestingly, Cowlishaw (1997) found that one group of chacma baboons was actually more likely to forage in areas that exhibited high food availability as well as increased predation risk. Cowlishaw (1997) theorised that these baboons were most likely forced to feed in such high risk areas due to living in larger groups. Contrastingly, Cowlishaw (1997) also found that a baboon group that contained fewer individuals (and only one male) was also more likely to feed in high risk areas. In this instance, he hypothesized that this group was forced into such high risk areas as a means to avoid by the threat imposed by larger rival groups (Cowlishaw, 1997) .

In addition to predation risk, there is evidence that such spatial avoidance strategies are employed when faced with intergroup competition (Cowlishaw, 1997; Da Cunha and Byrne, 2006; Markham *et al.*, 2013; Kumara *et al.*, 2014). Many social primate species exhibit territoriality to some extent and may compete for not only essential resources (food, water, and sleeping sites) but also reproductive opportunities (Samuel, 1983; Cowlishaw, 1998; Kappeler and Fichtel, 2012). In addition, aggressive encounters between groups have the potential to lead to physical violence, and death. Given these potential risks, spatial avoidance due to reproductive competition in primates has been found in baboons (Cowlishaw, 1997; Markham *et al.*, 2013), lion tailed macaques, (*Macaca silenus*) (Kumara *et al.*, 2014), and black howler monkeys (*Alouatta caraya*) (Da Cunha and Byrne, 2006). Markham (*et al.*, 2013) found that despite extreme home range overlap, yellow baboons residing in Ambsoli National Park (Kenya) practised short term spatial avoidance strategies particularly during periods in which females were fertile (and when aggressive encounters are more likely to occur). Therefore, spatial avoidance in primates may primarily be effective towards preventing (potentially fatal) conflict between different groups as well as reducing the reproductive success of rivals.

1.3 Furthering Our Understanding of Primate-Predator Interactions

Although predation is considered to play a fundamental role in both the behavioural ecology and evolution of primates, the direct assessment on how primates respond to the threat imposed by their local predators has been understudied. Most studies that assess primate-predator interactions are limited to focusing on the antipredator responses (i.e. spatial avoidance, vigilance, and distribution of alarm calls) exhibited by the focal primate species with having very little direct knowledge on where the predators are more likely to occur (Campos and Fedigan, 2014; Coleman and Hill, 2014). Although such research is undoubtedly important, the exclusion of predators in studies whose aims are to identify antipredator responses is inherently troublesome. By ignoring the whereabouts and direct probability of where local predators are likely to occur, researchers have the inability to directly correlate whether antipredator strategies used by primates actually reflect direct risk on the

landscape. This is primarily because prey perception of risk may not necessarily reflect where their predators are more likely to occur or hunt. As such, failing to account of factors such as landscape attributes or predator locations when assessing the landscape of fear may lead to inaccurate "mismatching" between perceived and actual risk (Gaynor *et al.,* 2019).

One example where both focal primate and predator species are simultaneously monitored came from Isbell and colleagues (2017) research on encounter rates between two species of primates (vervet monkeys and baboons) with leopards. In this instance, all three species were monitored for a period of 14 months with the aid of telemetry equipment (such as GPS collars and accelerometers). Although their study provided-detailed information on the frequency of encounter rates and the overall rarity of predation events on primate species, it did not assess how the primate species studies adapted to such risks over long periods. An additional example derives from Stanford (2002), who the assessed predator-prey dynamics between red colobus monkeys (*Piliocolobus tephrosceles*) and chimpanzees (*Pan troglodytes*). residing in Gombe National Park, Tanzania. In this instance, red colobus monkeys did not spatially avoid areas where the risk posed by predation was likely to occur but instead engaged in antipredator behaviours such as alarm calling and communal defence.

This thesis sets out to assess long term antipredator and spatial decisions in baboons using not only primate behavioural data but also through a thorough understanding of the behavioural ecology from their principal predator, the leopard. Unlike previous research, I hoped to understand whether antipredator strategies such as vigilance, alarm calls, and spatial avoidance in primates directly correlate with the actual probability of encountering their predator. Accomplishing this required a complete understanding on activity patterns and habitat selection for the leopards at the same study site as the baboons. The introduction of predator data to assess space use and antipredator behaviour in primates is not only novel yet also can also provide valuable insight regarding how predation risk and fear may potentially overlap with one another (Gaynor *et al.,* 2019).

While the utilisation of predator data is undoubtedly useful for understanding baboon space use, it is also acknowledged that baboon movement patterns may also possibly be influenced by other factors ranging from seasonally shifting levels of food availability to intergroup competition (and not just predation). By accounting for these variables, I hoped to further our understanding of how baboon spatial and behavioural patterns may be explained by multiple components of their environment.

1.4 Thesis Aims

The central aim of this thesis is to independently assess the behavioural ecology of chacma baboons as well as their principal predator, the leopard, within the western Soutpansberg Mountains, South Africa. To assess the spatial-temporal behaviours of both predator and prey is not only rare but is essential towards understanding both.

Although specific aims are presented in their respective chapters, I hoped to specifically assess the following:

1. The factors determining leopard range use (Chapter 3).
2. The factors that influence leopard movement behaviour and how it is distributed throughout the diel cycle (Chapter 4).
3. The factors influencing baboon space use (Chapter 5).
4. Factors that influence baboon vigilance (Chapter 5).
5. Factors that influence baboon behaviour across the diel cycle (Chapter 6).

To meet these aims, I use a combination of localised environmental data along with telemetry and activity data deriving from GPS collars and dual axis accelerometers to attain a greater understanding on spatial and temporal variation of habitat selection and movement patterns for leopards. The leopard data, along with environmental data and spatial and behavioural data from chacma baboons allow me to provide a detailed examination of how these primates spatially utilise their environment in response to seasonality, perceived risk, and food availability. Finally, I assess whether abiotic and biotic factors influenced nocturnal activity patterns in baboons.

1.5 Thesis Outline

Chapter 2 focuses on methodology and provides information on the study site and the two focal species, as well as detailed overview on the interaction between leopards and chacma baboons both at the study site and other locations throughout Africa. In chapter 3, I assess resource selection functions (RSFs) for leopards within the western Soutpansberg Mountains to determine the primary environmental variables that influence where they are likely to establish home ranges as well as where they reside and hunt within their home ranges. In chapter 4, I use data deriving from both GPS collars and dual axis accelerometers to examine how biotic and abiotic factors influence spatial and temporal patterns in activity for leopards residing within the study site. In chapter 5, I investigate whether baboons spatially avoid areas that they perceive to be risky and whether such perceived risk is driven by the probability of encountering leopards (through RSFs) and intergroup encounters. In addition, I also analyse both annual and seasonal space use patterns in baboons following to perceived risk, potential threats (leopards and intergroup encounters) and food availability. Finally, with the aid of both spatial and behavioural data, I investigate whether vigilance levels in baboons vary spatially in response to the probability of encountering leopards, competing baboon groups, and the periphery of their home range. In chapter 6, I evaluate whether baboons exhibit activity patterns at night and if such patterns are influenced by seasonal variation in day length, weather patterns, and lunar luminosity. I conclude in chapter 7 by discussing my findings, methodological limitations, and presenting suggestions for future research.

Chapter 2: Materials and Methods

2.1 Study Species

2.1.1 Chacma Baboons

The chacma baboon (*Papio ursinus*) is a large, diurnal, and terrestrial species of primate whose range includes numerous habitats throughout most of southern Africa (Estes, 1991) (Figure 2.1). Like other members of *Papio,* chacma baboons are extremely sexually dimorphic in terms of body size, with adult males having the potential to weigh up to 80% more than adult females (Isaac, 2005). The mean weight for wild adult males is typically up to 30 kg, whereas females tend to weigh approximately 15 kg (Bulger and Hamilton, 1987). Adult males have large canines (3.6 cm for mean canine length) (Hamilton and Bulger, 1990) that are often used to display a threatening demeanour towards, or as weapons in physically aggressive interactions with, other males (Chevalier-Skolnikoff, 2006). Females exhibit colourful sexual swellings throughout the perineal area that often peak around ovulation (Domb and Pagel, 2001).

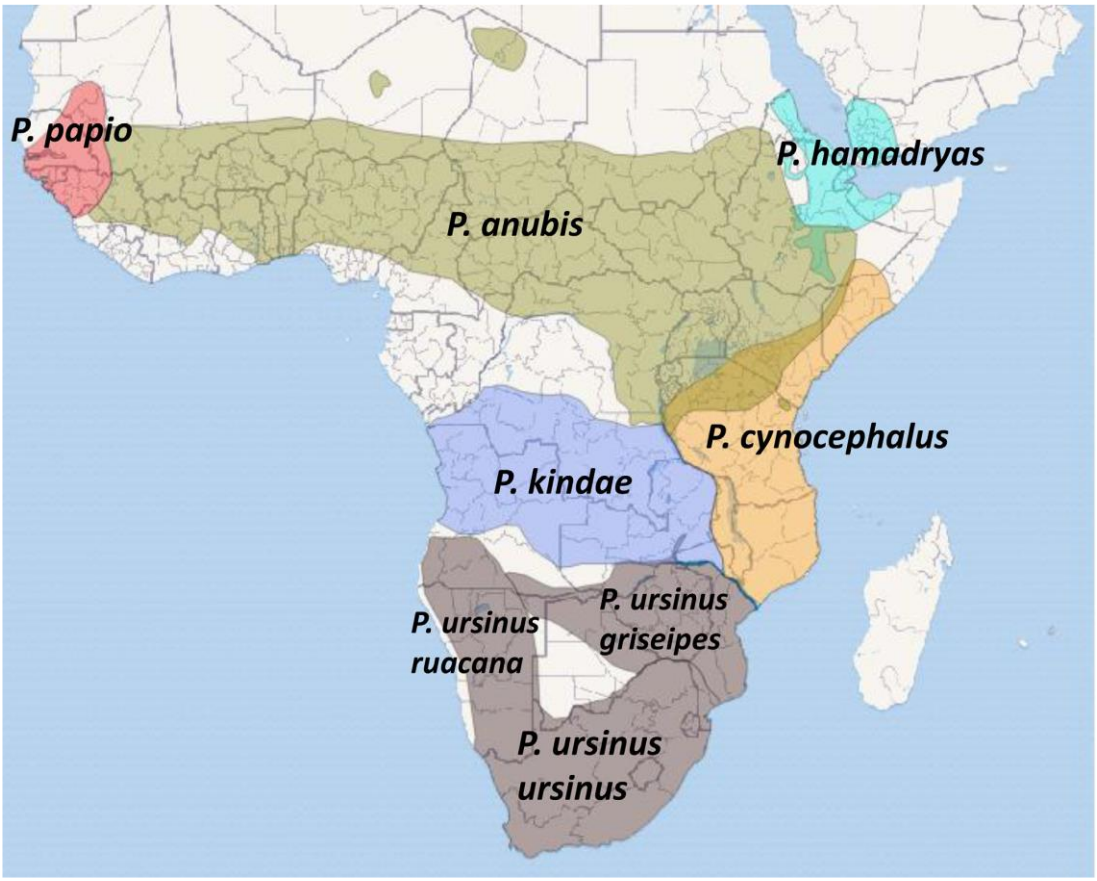

Figure 2.1 Natural extent of Papio throughout Africa ((Martinez *et al.*, 2019).

Baboons of both sexes typically reach sexual maturity by roughly five years of age (Altmann, Altmann and Hausfater, 1981). In females, this stage is signified by the first occurrence of menarche (Altmann, Altmann and Hausfater, 1981), whereas, in males, this is primarily indicated by the enlargement of the testes (Alberts and Altmann, 1995). While baboons do not typically have birthing seasons, chacma baboons in the Drakensburg Mountains (South Africa) may give birth more often during the wet season (Lycett, Weingrill and Henzi, 1999). After approximately six months of gestation (Cheney and Seyfarth, 2008), chacma baboons will usually produce one offspring biannually. However, such intervals are prone to variability due to localised environmental conditions (Hill, Lycett and Dunbar, 2000), group size (Hill, Lycett and Dunbar, 2000), and dominance rank (Cheney *et al.*, 2004; Silk, Willoughby and Brown, 2005).

Chacma baboons tend to live in complex, multi-male-multi-female groups that vary in size from as few as four (Henzi, Lycett and Piper, 1997) to over a hundred individuals (Cheney and Seyfarth, 2008). While female baboons will

often remain with their natal troop for the entirety of their lives, males usually leave at the onset of adulthood (Barrett and Henzi, 2008). As such, baboon societies are primarily structured around females and their closest kin - who may form closely-knit matrilineal subgroups within the troop (Silk, Altmann and Alberts, 2006).

Around the time of ovulation, females will often initiate a short term consortship with an adult male. During this period; both individuals frequently engage in activities such as copulating and grooming one another (Cheney and Seyfarth, 2008). In addition, sexually inactive females may form long-term bonds (often known as 'friendships') with unrelated adult males (Palombit, Cheney and Seyfarth, 2001; Palombit, 2009). In such instances, males and females will not only reciprocally groom each other, but males may also handle the females' infants (Palombit, 2009). Such friendships with males may benefit female baboons by providing the infant with protection from attacks by other males, as well as promoting bonds between male friends and offspring (Busse and Hamilton, 1981; Lemasson, Palombit and Jubin, 2008; Palombit, 2009). Outside of friendships, males do not create bonds with juveniles, infants, or other adult males (Palombit, 2009).

Given their widespread range throughout Southern Africa, chacma baboons have been recorded as successfully adapting to a variety of different habitats, including mountains (Whiten, Byrne and Henzi, 1987; Henzi, Byrne and Whiten, 1992), savannahs (Weingrill *et al.*, 2003), deserts (Hamilton III, Buskirk and Buskirk, 1976; Hamilton, 1985; Cowlishaw, 1997), and swamps (Hamilton III, Buskirk and Buskirk, 1976). In addition, chacma baboons can also be found residing in close proximity to humans in both rural and semi-urban settings (Hoffman and O'Riain, 2011). In such instances, they are often regarded as pests due to their tendency to raid agricultural areas and are frequently retaliated against through either lethal or non-lethal methods (Hill, 2000; Hill and Webber, 2010). Despite retaliation against crop-raiding baboons being commonplace throughout Southern Africa, chacma baboons are not considered to be under threat from extinction and therefore have the conservation status of "least concern" by IUCN (Hoffmann and Hilton-Taylor, 2008).

It seems likely that the biogeographical range of chacma baboons is partially due to their dietary flexibility. Chacma baboons have been observed consuming a variety of different food items across their range, including plant (seeds, fruit, grasses, leaves, tubers) and animal matter (Buskirk and Buskirk, 1978; Codron *et al.*, 2006; Johnson *et al.*, 2013). Despite this, chacma baboons living in the most southern parts of Africa are often seasonally constrained by not only day length but also food availability, and, as such, they will respond to such restrictions in winter months by both maximising foraging time (and efficiency) and feeding on lower quality food items (Hill, Barrett, Gaynor, A. Weingrill, *et al.*, 2003; Hill *et al.*, 2004; van Doorn, O'Riain and Swedell, 2010).

Chacma baboons have relatively large home ranges compared to other African primates, but, like other species, will often preferentially use certain areas in their home ranges (Altmann and Altmann, 1973).The factors that influence how baboons use their home ranges include resource distribution (Hoffman and O'Riain, 2011), distance to sleeping sites (Anderson, 1998, 2000), and predation risk (Altmann, 1974; Cowlishaw, 1997). Additionally, variation in food and water availability influence the size of home ranges for baboons living in different environments, with those living in more arid or otherwise adverse habitats often having larger home ranges and travelling further distances (Cowlishaw, 1997) compared to those living in areas with steady or near-constant food supplies, such as near human settlements and agricultural areas (Hoffman and O'Riain, 2012).

While chacma baboons are not known to be territorial, with some groups sharing 50% of their home range with other troops (Anderson, 1981), baboons residing in habitats that are either scarce in resources (i.e. Namib Desert, Namibia) or have high population densities (Okavango Delta, Botswana) defend their home ranges' edges from competing groups (Hamilton III, Buskirk and Buskirk, 1976). In addition, intergroup encounters tend to vary between toleration while feeding in somewhat close proximity to avoidance or antagonism (Cowlishaw, 1995; Kitchen, Cheney and Seyfarth, 2004).

Chacma baboons are susceptible to predation from numerous species across their range. Predators such as the African rock python *(Python seba)* (Tomlin,

2016), crowned eagle (*Stephanoaetus coronatus*) (Mitani *et al.*, 2001), and Verreaux's eagle (*Aquila verreauxii*) (Zinner and Peláez, 1999) primarily pose a threat to juveniles, and they are often too small to efficiently hunt adults. In contrast, large mammalian carnivores (such as felids) present the biggest threat to both juveniles and adults (Busse, 1980; Cowlishaw, 1994; Cheney *et al.*, 2004; Jooste *et al.*, 2013; Matsumoto-Oda, 2015). For example, lions (*Panthera leo*) have been found to opportunistically hunt all baboon age-sex classes, despite variability in body size and, thus, profitability (Busse, 1980). While spotted hyaenas (*Crocuta crocuta*) occasionally hunt solitary baboons, there is little evidence to suggest that they pose as a substantial threat (Cheney *et al.*, 2004). This is most likely because hyenas will often forage alone and consequently have the potential to be mobbed by a baboon group. Likewise, as baboons sleep in either trees or cliffs at night, it is plausible that, without substantial climbing adaptations, hyenas may not have access to baboons, who often sleep in elevated and insulated places such as cliffs or trees. Similarly, African wild dogs have yet to be recorded hunting baboons (Cheney *et al.*, 2004).

Although baboons are considered to be a primary prey item of leopards, it should be noted that the size, aggressiveness, and the ability to mob may act to discourage leopards from hunting baboons to avoid incurring substantial risk of bodily harm or death (Hayward, Henschel, O'Brien, Hofmeyr, Balme and G. I H Kerley, 2006) . As such, baboons appear to be a less significant part of leopards' overall dietary composition compared to prey such as ungulates (Hayward, Henschel, O'Brien, Hofmeyr, Balme and Kerley, 2006).

Nevertheless, leopards still appear to be the primary predators of baboons in areas where the two species co-exist (Hayward, Henschel, O'Brien, Hofmeyr, Balme and Kerley, 2006), and they have been recorded as being twice as successful with hunting baboons compared to lions (Cowlishaw, 1994). Unlike lions, who often predate on baboons during the day (Busse, 1980; Cowlishaw, 1994), leopards are known to hunt baboons throughout the diel cycle and are most successful at hunting baboons at dawn, dusk, and night, when the latter are in proximity to their sleeping sites (Busse, 1980; Hamilton, 1982; Cowlishaw, 1994; Cheney *et al.*, 2004). Such a preference for nocturnal attacks

may also be due to leopards being vulnerable to retaliation during diurnal hours when baboons are active (Busse, 1980; Cheney *et al.*, 2004). In contrast, nocturnal attacks can be severely debilitating for baboons, as leopards may repeatedly attack the same sleeping site at night (Cheney *et al.*, 2004), relying on surprise as well as the baboon's limited night vision and hesitance to descend from their sleeping site (Busse, 1980; Cowlishaw, 1994).

Although most leopard attacks having been recorded at night, several instances of diurnal attacks have been reported (Cowlishaw, 1994; Cheney *et al.*, 2004; Jooste *et al.*, 2013). For example, Jooste (*et al.,* 2013) found that female leopards in the Waterberg Mountains, South Africa were more likely to predate baboons during the daylight hours (70%). In this instance, baboons were predated on more than usual compared to other sites, which suggests that some leopards in the Waterberg Mountains learn to hunt baboons at an early age (Jooste *et al.*, 2013).

Unlike lions, leopards have been found to primarily hunt adult baboons (Cowlishaw, 1994). Cowlishaw (1994) concluded that leopards in Namibia were more likely to predate on adult male baboons than females due to the former's habit of sitting on the edge of the group (where they have fewer near neighbours) and leaving the troop upon adulthood. Despite this, several other studies have found that while adults are still preferred, differences in mortality between sex classes are either minimal or non-existent, and, therefore, most leopard populations may not necessarily have a direct preference for one sex over the other (Cheney *et al.*, 2004; Jooste *et al.*, 2013). As ambush predators, leopards primarily rely on coverage to pursue their prey (Sunquist and Sunquist 1989; Bailey 1993) and, consequently, baboons' susceptibility to predation may vary depending on the habitat type (Boinski, Treves and Chapman, 2000). Since essential resources (i.e. food patches, water sources) often overlap with areas that are perceived to be riskier, baboons may decrease the amount of time spent in such areas (Altmann and Altmann, 1973; Cowlishaw, 1997). For example, baboons in Amboseli National Park (Kenya) were known to only utilise high-risk areas (where alarm calling is more frequent) when high quality resources are present and avoid such locations

otherwise (Altmann and Altmann, 1973). Additionally, Cowlishaw (1997) found that baboons in Namibia were also less likely to avoid areas of high risk and low visibility, and prefer to engage in social behaviours such as grooming in parts of their home ranges that allow for greater visibility. Baboons venturing into high-risk areas may also minimise group spread as a means to decrease the distance between members and the group's periphery, thereby facilitating mobbing during an attack (Lima and Dill, 1990; Boinski, Treves and Chapman, 2000).

Actual attempted predation events by leopards (or other terrestrial carnivores) on baboons have been recorded to be highly chaotic with baboons either retaliating through mobbing (if during the day), eliciting alarm calls, or running to the closest nearby refuge (Busse, 1980; Cowlishaw, 1994; Cheney *et al.*, 2004). Baboons may then avoid areas where successful predation events have taken place for several days (Matsumoto-Oda, 2015). The days following an attack have been shown to have both physiological and behavioural implications for surviving group members, with such effects being especially pronounced in the predated baboon's close relatives (Engh *et al.*, 2006). For example, female chacma baboons who have recently lost a close companion or relative due to predation often exhibit elevated glucocorticoid levels, potentially experiencing social isolation, and, as a result, they attempt to establish new social bonds by seeking new grooming partners and increasing grooming rates (Engh *et al.*, 2006). These results suggest that, like perceived predation risk, actual predation events also have physiological and behavioural consequences (Engh *et al.*, 2006).

2.1.2 Leopards

Ranging throughout Sub-Saharan Africa, the Middle East, and into East Asia, the leopard (*Panthera pardus*) is one of the most widespread large carnivore species (Uphyrkina *et al.*, 2001; Jacobson *et al.*, 2016; Stein *et al.*, 2016) and the most widespread large felid on the African continent (J. C. Ray, Hunter and Zigouris, 2005) (Figure 2.2). Leopards have successfully adapted to an array of environments, such as deserts (Bothma, Van Rooyen and Le Riche, 1997; Perez, Geffen and Mokady, 2006), temperate forests (Karanth and Sunquist, 2000; Wang and Macdonald, 2009), rainforests (Henschel, 2007, 2008; Simcharoen *et*

al., 2008) and woodland savannahs (Cavallo, 1991; Bailey, 1993), as well as the edges of urban areas (Athreya *et al.*, 2013, 2016). The biogeographical success of leopards is likely due, in part, to their extremely catholic diet and elusive nature (Hayward, Henschel, O'Brien, Hofmeyr, Balme and G. I H Kerley, 2006).

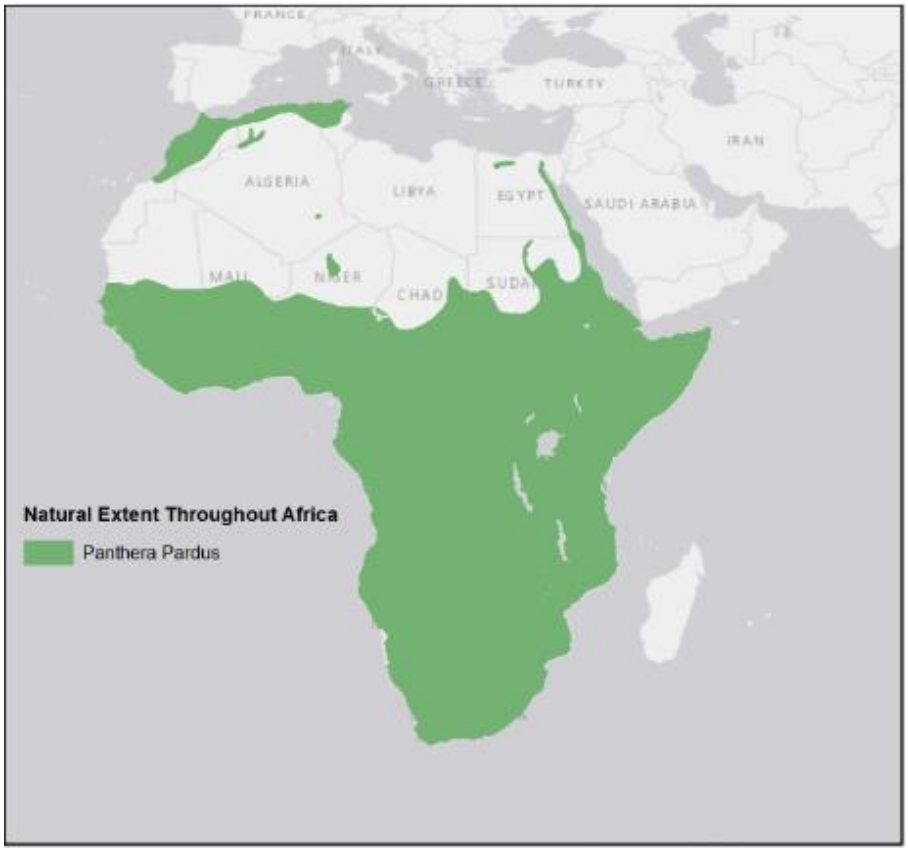

Figure 2.2 Range of *Panthera pardus* throughout Africa (Range layer derived from IUCN and implemented in ArcGIS).

Leopards are sexually dimorphic, with males being considerably more robust than females (Bailey, 1993). One study on 30 captive adult leopards finds males to be up to 70% heavier and 10% longer than females, with older males, on average, weighing up to 63 kg, compared to 37 kg for females (Bailey, 1993). In addition, the average weight for leopards can vary significantly depending on habitat and prey availability; leopard populations that rely on smaller species tend to also be smaller in mass and have lower reproductive rates (Grobler and Wilson, 1972).

Female leopards typically reach sexual maturity around the age of three (Bailey, 1993; Owen, Niemann and Slotow, 2010). They are polyestrous and will cycle regularly until conception (Bailey, 1993; Owen, Niemann and Slotow, 2010).

During such periods; adult leopards will often pair up and copulate frequently for between 4 and 96 days (Bailey, 1993). Gestation length in leopards has been recorded to last from 95 to 106 days, with females typically giving birth to 1 to 6 cubs (Owen, Niemann and Slotow, 2010; Stein and Hayssen, 2013). While females can reproduce throughout the year, most births that occur in South Africa take place during the rainy season (Bailey, 1993). As lactating and rearing cubs is considered to be energetically costly (Clutton-Brock, Albon and Guinness, 1989), such birthing peaks can be attributed to abundance of prey (Balme *et al.*, 2013). In addition, higher vegetation coverage during such periods aids in hunting and provides sufficient coverage for cubs (Bailey, 1993; Balme *et al.*, 2013). Cub mortality is relatively high, with Bailey (1993) reporting a loss of 41 to 50% of cubs within the first year alone (Bailey, 1993). Primary causes of cub mortality include infanticide and predation by other predators, (Bailey, 1993; Balme *et al.*, 2013; Stein and Hayssen, 2013). Juvenile leopards typically stay with their mother for 12 to 18 months (Bailey, 1993). Following this, female offspring will often share a part of their home range with their mothers, whereas males will completely disperse (Stein and Hayssen, 2013).

While male leopards tend to have larger home ranges than females (Bailey, 1993; Stein and Hayssen, 2013), space use patterns in leopards may also vary depending on habitat and prey abundance, with large home ranges usually having low prey availability and small home ranges having good hunting coverage and prey densities (Stein and Hayssen, 2013). The home range for one male leopard in the arid Kalahari Desert has exceeded 2000 km^2 (Bothma and Le Riche, 1984), with other large home ranges in Africa recorded in Kaudam National Park, Namibia, (451 km^2 for males and 188 km^2 for females) (Stander *et al.*, 1997), as well as in the mountains of Cape Provence (South Africa) (388 km^2 for males and females) (Norton and Lawson, 1985). Interestingly, leopards residing in arid North-central Namibia in Kaudam National Park have relatively small home ranges (108 km^2 for males and 50 km^2 for females) (Stein *et al.*, 2011). The authors attributed the smaller home ranges to the abundance of prey such as greater kudu (*Tragelaphus strepsiceros)* and warthog *(Phacochoerus aethiopicus)* (Stein *et al.*, 2011). The smallest home ranges for

leopards often occur in forested and rocky areas or where prey abundance is generally high (Stein and Hayssen, 2013). For example, home ranges are particularly small in prey-rich areas such as Kruger National Park (38 km^2 for males and 15 km^2 for females) (Bailey, 1993), Lolldaiga Hills, Kenya *(*33 km^2 for males and 14 km^2 for females) (Mizutani and Jewell, 1998) and Serengeti National Park, Tanzania, (15.9 km^2) (Bertram, 1982). Leopard home range sizes may also fluctuate seasonally in response to the movement and behaviour of their main prey (Bailey, 1993). For example, Bailey observed that leopards in Kruger National Park were more likely to fluctuate the size of their home ranges in accordance to the seasonal movements of impala (*Aepyceros melampus*) (Bailey, 1993).

Spatial use patterns in leopards may also vary by reproductive status, with adult females shifting their home range sizes in accordance to the age and mobility of their cubs (Steyn and Funston, 2009). Additionally, with the exclusion of exploratory movements, home range size can be influenced by age, with sub-adult males typically having home ranges that are similar in size to an adult female's (Bailey, 1993). Leopards have been shown to be selective regarding where they choose to establish home ranges, with prey abundance (Bailey, 1993), catchability (Balme, Hunter and Slotow, 2007), (Vanak *et al.*, 2013) and habitat quality (Fattebert *et al.*, 2015) all being considered possible factors that influence where leopards choose to reside (Chapter 3). Balme (*et al.,* 2007) found that leopards in Phinda Private Game Reserve (South Africa) were more likely to reside in areas where intermediate to high vegetation provided them with sufficient coverage to stalk prey.

Although the activity patterns of leopards are generally regarded as crepuscular or nocturnal (Hayward, Henschel, O'Brien, Hofmeyr, Balme and G. I H Kerley, 2006) (Chapter 4), several studies have shown that they, in fact, may be more fluid in their movement patterns than previously thought**.** For example, although leopards in Kruger National Park are most likely to exhibit nocturnal activity patterns, they have been observed to hunt more frequently in the early morning hours and occasionally during the day (Bailey, 1993). Similarly, diurnal activity schedules have been recorded in leopards in the Cederberg (Norton and

Henley 1987; but see Martins and Harris 2013) and in Taï National Park (Ivory Coast) (Jenny and Zuberbühler, 2005). In contrast, leopards in more open or arid areas were found to exhibit nocturnal activity. Indeed, leopards residing in the Kalahari (Bothma and Le Riche, 1984), Namibia (Stander *et al.*, 1997), and the Maasai steppe (Tanzania) (Kissui, 2008) were predominantly active during nocturnal or crepuscular hours. It is likely that the various activity patterns exhibited by leopards may be due to specific environmental conditions. For example, it has been hypothesised that leopards residing in forested environments may be diurnal as a means to hunt during the time periods in which their prey are most active (Jenny and Zuberbühler, 2005). Likewise, leopards in forested environments can be diurnally active due to the high amount of hunting coverage that is characteristic of such habitats (Jenny and Zuberbühler, 2005b; Hayward, Henschel, O'Brien, Hofmeyr, Balme and G. I H Kerley, 2006). The nocturnal activity patterns of leopards in more open environments may be due to either increased stalking coverage during such time periods or to avoid competition with dominant carnivores, such as lions (Hayward and Slotow, 2009).

In Africa alone, leopards have been reported to consume up to 92 species, from small arthropods and rodents to large ungulates (Hayward, Henschel, O'Brien, Hofmeyr, Balme and G. I H Kerley, 2006; Balme, Hunter and Slotow, 2007). While the mean weight for prey items ranges between 10 and 40 kg, leopards generally prefer small- to medium-sized ungulates ranging between 23 and 25 kg that primarily live in small herds and thick vegetation (Hayward, Henschel, O'Brien, Hofmeyr, Balme and G. I H Kerley, 2006). Leopards are solitary hunters, and ungulates within such a body mass range are relatively easy to catch and provide very little risk of injury (Hayward, Henschel, O'Brien, Hofmeyr, Balme and G. I H Kerley, 2006).

Although leopards typically prefer to predate on medium-sized ungulates when available, they will often compensate in habitats where such species are scarce by predating on smaller prey (Hayward, Henschel, O'Brien, Hofmeyr, Balme and G. I H Kerley, 2006). This has been observed in other solitary felids, including pumas (*Puma concolor*) (Iriarte *et al.*, 1990) and snow leopards (*Panthera*

uncia) (Schaller, Junrang and Mingjiang, 1988). For example, Schaller (*et al.,* 1988) found that snow leopards residing in China's Qinghai province relied on marmots (*Marmota sp*.) for 45% of their food intake during summer months. This dietary switch to smaller prey has also been recorded by Ott (2004) who finds that rodents make up 9% of the diet for leopards residing in the Baviaanskloof Wilderness Area of South Africa where wild ungulates were rare yet livestock were common. Additionally, a scat analysis by Ray and Sunquist (2001) suggested that leopards living in the heavily forested Dzanga-Sangha Reserve (Central African Republic) had a mean prey weight of 7.3 kg and primarily relied on small duikers, rodents, monkeys and pangolins. In this instance, however, the authors argued that such selectivity may relate to the abundance of such fauna rather than the reduction of medium-sized mammals.

Like most other large felids, leopards are ambush predators and primarily rely on stealth and stalking coverage to successfully subdue their prey (Bailey, 1993; Marcella, 2004; Stein and Hayssen, 2013). The distance over which leopards stalk a prey item may vary depending on habitat type and species. Bothma and Le Riche (1989) found that leopards in the arid and relatively open Kalahari Gemsbok National Park of South Africa stalked their prey for relatively long distances in order to maximise a successful kill, a practice that they refer to as "optimal positioning" (Bothma and Le Riche, 1989). In such instances, leopards did not only rely on vegetation cover, as they also preferred advantageous wind conditions and high vantage points in order to keep track of their prey's location from great distances (Bothma and Le Riche, 1989). The mean stalking distance for leopards engaging in optimal positioning was recorded as 1542.5 metres (Bothma and Le Riche, 1989), and optimal positioning was more likely to occur when leopards hunted large and especially vigilant or dangerous prey, such as gemsbok (*Oryx gazella*) and ostrich *(Struthio camelus*) (Bothma and Le Riche, 1989).

As ambush predators, leopards prefer to hunt in densely vegetated areas and, therefore, often tend to avoid open habitats where their ability to successfully stalk at close range is limited (Hayward, Henschel, O'Brien, Hofmeyr, Balme and G. I H Kerley, 2006). Pitman and colleagues (2013) found that 96% of kills

taking the Waterberg Mountains occurred in areas with the greatest vegetation density, with the leopards avoiding all other habitats to hunt in. Similarly, Bailey (1993) shows that leopards in Kruger National Park were more likely to kill their prey in either dense riparian vegetation or medium to dense thorn patches rather than open areas.

Despite preferring hunting in areas exhibiting high vegetation coverage, it should be noted that such regions may also provide a slight disadvantage for stalking leopards. As leopards primarily rely on sight (compared to olfactory cues) and stealth while pursuing prey, areas that exhibit incredibly high vegetation may obstruct vision while simultaneously alerting prey through creating noise (Balme, Hunter and Slotow, 2007). Balme and colleagues (2007) observed that leopards in the Phinda Game Reserve of South Africa are more likely to hunt in areas featuring intermediate vegetation coverage despite the fact that such habitats did not have the highest prey abundance in the study area. In this instance, the researchers suspect that leopards at Phinda Game Reserve had balanced reduced encounter rates with coverage that is sufficient for prey to be stalked undetected from visual obstructions (Balme, Hunter and Slotow, 2007).

Although the "stalk-chase-kill" sequence seems to be a primary hunting method for leopards across their range, populations in more closed or heavily forested environments have been shown to prefer hunting prey through a second method, the "ambush-pounce" (Hart, Katembo and Punga, 1996; Jenny and Zuberbühler, 2005b; Balme, Hunter and Slotow, 2007). Hart (*et al.,* 1996) found that leopards residing in the Ituri Forest (Democratic Republic of Congo) often concealed themselves in vegetation layers close to fruiting trees that attracted prey like monkeys, red river hogs (*Potamochoerus porcus*) and duikers and then ambushed once they come within a few metres. This method was also recorded among leopards residing in The Ivory Coast (Jenny and Zuberbühler, 2005) as well as those living in the dense woodlands found in Londolozi Private Game Reserve, South Africa (Hes, 1991). It is quite possible that the diurnal activity patterns found in leopards in forested environments may be partially explained

by hunting techniques (i.e. ambush-pounce) that require the prey to be active and mobile.

Leopards kill their prey by biting the nape of their neck or by puncturing the brain case with their canines (Stein and Hayssen, 2013). In general, it seems that leopards are more likely to bite the nape of large prey, as a means to avoid horns, whereas puncturing the skull is a method often employed for killing smaller or hornless prey (Stein and Hayssen, 2013) (Figure 2.3). Following the kill, leopards will either eat the prey immediately or, most frequently, drag their kill into a densely covered area to feed undisturbed (Bailey, 1993). Although leopards will often drag their prey less than 100 metres away from the kill site (Bailey, 1993), distances may vary significantly depending on the environment. For example, females with cubs and male leopards in the arid Kalahari have reportedly dragged their prey an average of 742, and 410metres, respectively, in order to find sufficient coverage to feed (Bothma and Le Riche, 1984). In contrast, leopards in the rainforests of Sri Lanka only dragged their prey 11 to 12 metres (Eisenberg and Lockhart, 1972).

Figure 2.3 Posterior view of four puncture marks found on an adolescent bushpig (*Potamocherus larvatus*) killed by an adult male leopard in the western Soutpansberg Mountains, South Africa. Scale unavailable.

Besides dragging their prey and feeding on the ground, leopards have been observed to hoist their prey onto trees as a means to cache their kills (Bailey,

1993; Stein, Bourquin and McNutt, 2015; Balme *et al.*, 2017). It has been suggested that this behaviour allows them to spatially and temporally overlap with dominant carnivores that are less equipped at climbing, such as spotted hyenas, without risking kleptoparasitism (Balme *et al.*, 2017). Leopards in Kruger National Park, where spotted hyena densities are high, have been recorded to hoist their kills (Bailey, 1993). In contrast, leopards found near agricultural areas in Namibia (where they are the largest predator in the area) only hoist their prey 12% of the time (Stein, Bourquin and McNutt, 2015). Leopards found in the Kalahari cache their prey 17% of the time, and primarily only after they are interrupted by a dominant carnivore (Bothma and Le Riche, 1984). Interestingly, Stein (*et al.,* 2015) record that leopards residing in Botswana only hoisted their kills 38% of the time, despite the presence of dominant carnivores like spotted hyenas, wild dogs, and lions. As hoisting is costly in terms of energy, the researchers theorised that such a low proportion of hoisted kills reflects the fact that leopards in the study area only did so in areas of immediate risk and high visibility, rather than just the perceived risk from kleptoparasitism (Stein, Bourquin and McNutt, 2015). Alternatively, they have been recorded caching their prey in dolomite caves when such features are available, and they may have contributed to the accumulation of Plio-Pleistocene faunal remains at hominin bearing sites, such as Sterkfontein (de Ruiter and Berger, 2000).

Bailey (1993) recorded that leopards in Kruger National Park usually consumed carcasses in the same sequence, starting from the posterior sections of the carcass (i.e. hindquarters, groin, and abdomen) and then moving up to the forelimbs, shoulder, and skull. Although varying with prey size, leopards may spend up to several days feeding upon a carcass (averaging 2.4 days for 40 kills). Female leopards with cubs and adult males in poor health are more likely to spend more time feeding on carcasses compared to healthy adult males and females without cubs (Bailey, 1993). Sickly leopards also consume more skin and bones compared to healthy individuals (Bailey, 1993). Time intervals between kills have been shown to vary between sex and habitat with males typically resuming hunting 7.2 days after the last kill and females spending approximately 7.5 days before hunting again (Bailey, 1993). In contrast, adult

leopards that stalk over long distances (such as in the Kalahari) tend to kill every three days; this is even more reduced in desert females with cubs, who, on average, hunt every 1.5 days (Bothma and Le Riche, 1984).

Despite their adaptability and widespread range, leopards are classified as 'vulnerable' by the IUCN red list and have disappeared from approximately 48% of their former range in Africa (Jacobson *et al.*, 2016). Primary threats to leopard populations globally include habitat loss and fragmentation (Ray, Hunter and Zigouris, 2005; Swanepoel *et al.*, 2013), as well as persecution by humans (Treves and Karanth, 2003; Inskip and Zimmermann, 2009; Balme, Slotow and Hunter, 2010). In addition, the decline of primary prey species by 59% between 1970 and 2005 in 78 protected areas throughout Africa due to a commercial bush meat trade (Craigie *et al.*, 2010) may contribute to the decline of leopard populations throughout the continent. As most leopard populations in Africa reside in unprotected areas, it has been suggested that increased human encroachment into leopard habitats may significantly influence the further decline of the species across its range (Thorn *et al.*, 2013).

2.2 Study Site

2.2.1 Location

This research project was conducted from data collected at the Lajuma Research Centre in the western Soutpansberg Mountains, Limpopo Province, South Africa (23°06'45.14"S 29°11'37.10"E) (Figure 2.4). Characterised by its high levels of biodiversity, Lajuma was given Natural Heritage Site status in 1997. In 2009, the Soutpansberg Mountains were integrated into the United Nations Educational, Scientific and Cultural Organization's (UNESCO) Vhembe Biosphere Reserve (VBR). At approximately 30,701 km^2, the VBR includes numerous nationally recognised areas of cultural and ecological significance, such as the Makgabeng Plateau, Mapungubwe National Park, and World heritage site, several natural reserves, the Blouberg Mountains, as well as the northern portion of Kruger National Park (http://www.unesco.org/new/en/natural-sciences/environment/ecological-sciences/biosphere-reserves/africa/south-africa/vhembe/). In 2014, the western Soutpansberg was incorporated into the province-based Limpopo

Leopard Project (LLP), which sought to monitor and sustain leopard populations across Limpopo. (http://www.welgevonden.org/files/conservation/leopard_research/Leopard%20Annual%20Report%20Welgevonden%202014.pdf).

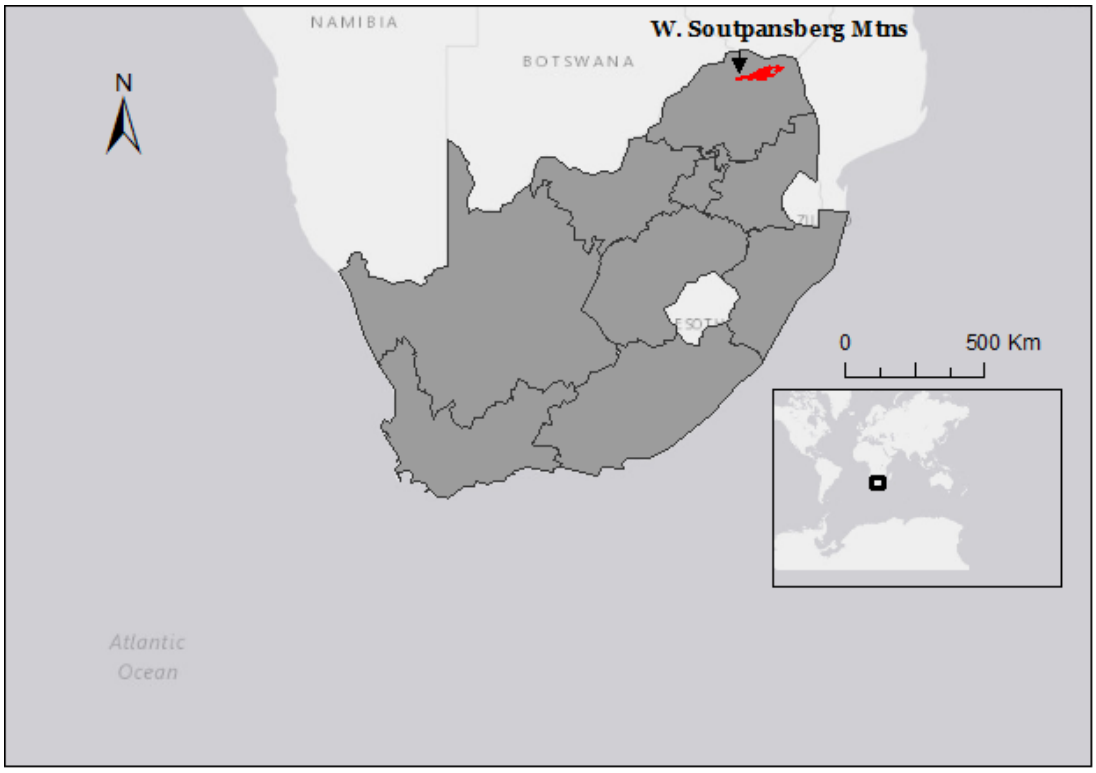

Figure 2.4 Image of South Africa (highlighted in dark grey) with the Soutpansberg Mountains highlighted in red. The arrow tip points to the study site at the western edge of the mountain range.

2.2.2 Topography and Geology

Spanning approximately 210 km from east to west as well as 60 km (at its widest) to 15 km (at its most narrow) from north to south, the Soutpansberg Mountains have a total surface area of approximately 6,800 km^2 (Hahn, 2006). Altitude in the region varies significantly from 250 m above sea level to its highest point, Lajuma, at 1748 m above sea level (Mostert *et al.*, 2008). Neighbouring the Soutpansberg Mountains to the west by 30 km are the Blouberg Mountains, which sport the highest elevation in the area at roughly 2,051 metres above sea level (Constant, 2014). Surrounding both mountain ranges are undulating lowlands with altitudes ranging from approximately 400 to 900 metres above sea level (Kirchhof *et al.*, 2010).

The initial strata (basaltic lava and sediments) that formed the Soutpansberg mountains were deposited roughly 1,800 million years ago as an east-west asymmetrical rift following a major collision between the northern Limpopo belt and southern Kaapvaal craton (Hahn, 2006). After a series of tectonic events during the Mesozoic, a successive ESE-WSW faulting ranging roughly 560 km caused a depression that resulted in a north-oriented dip and a south-oriented rise. As a result, the Soutpansberg Mountains have tall, vertical cliff lines facing the south and a 45° incline towards the north (Hahn, 2006).

The Soutpansberg contains dolerite, quartz sandstone, basalt, quartzite, sandstone and other major rock types (Hahn, 2006). Deriving from primarily weathered sandstone and quartzite, much of the soil is regarded as nutrient-poor, sandy and highly acidic (Hahn, 2006). Meanwhile, weathered basalt and dolerite comprises much of the nutrient-rich clay soils found in the area, and minerals found in Soutpansberg consist of quartz, salt, copper, tin and gold (Hahn, 2006).

2.2.3 Climate

The Soutpansberg Mountains have variable levels of precipitation and temperature throughout the range as a result of both topography and vegetation. However, in general, the climatic conditions exhibited are considered to be temperate/mesothermal, and with both cool/dry winters (May to August) and relatively wet/hot summers (December to February) (Kabanda, 2003). Temperatures in the Soutpansberg Mountains range from 16-40 °C in summer and 12-22 °C in winter (Figure 2.5) (Kabanda, 2003).

Precipitation in the Soutpansberg Mountains varies significantly, with the western portion receiving up to 340 mm of rain per year compared to the central region, which can receive up to 2,000 mm per year (Kabanda, 2003). Likewise, there is considerable variability found between the more arid northern slopes of the mountains, which receives approximately 400 mm of rain per year, and the south-central, which receive up to 1,800 mm of rainfall per year (Schulze *et al.*, 2008). Overall, the precipitation patterns throughout the mountain range are considered to be orographic, and result from moisture-ridden air south-eastern winds from the Indian Ocean that are eventually

wedged in the southern portion of the Soutpansberg as mist and rain (Hahn, 2006; Kirchhof *et al.*, 2010). As a result, the southern section of the mountains is considerably moister compared to the north.

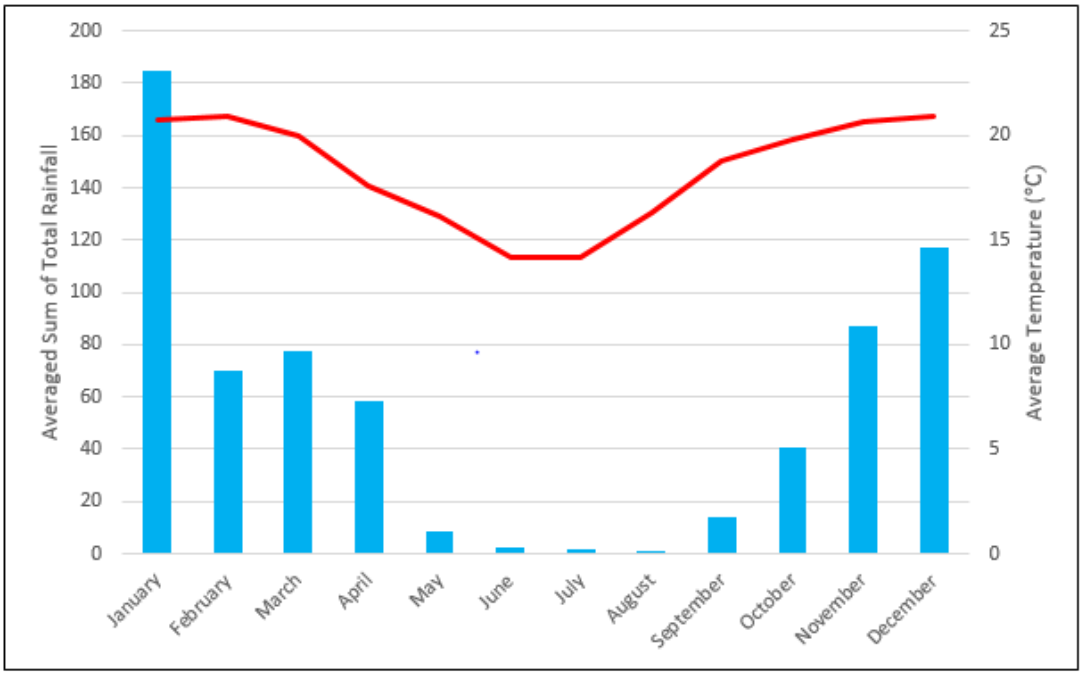

Figure 2.5 Combined monthly average temperature (blue column) and averaged sum of total rainfall (red kine) from 2012-2017 for the western Soutpansberg Mountains. Derived from an on-site weather station.

Winds in the Soutpansberg Mountains generally blow from east to west (Hahn, 2006). Convection currents are commonplace due to the difference in temperatures between the northern and southern portion of the mountains. However, as the severity of such currents is primarily due to the transition of the sun, such effects are generally considered to be seasonal (Hahn, 2006). Katabatic winds in the Soutpansberg often lead to a substantial drop in ambient temperatures; this is especially true after sunset during winter (Hahn, 2006), when narrow valleys throughout the range start to rapidly cool.

2.2.4 Flora

As a result of its complex topography, the Soutpansberg Mountains contain a diverse range of vegetation communities, and at least 2693 plant species, including 593 trees (Mucina and Rutherford, 2006). Due to its accessibility online and its compatibility with ArcGIS, vegetation communities classified by Mucina and Rutherford (2006) and adapted into the National Vegetation Map Project (http://bgis.sanbi.org/vegmap/project.asp) were utilised for this

research. Habitats defined by Mucina and Rutherford (2006) that intersect with both the study site and the focal animals' home ranges include (but also Appendix 1; Figure S1.1):

1. Mountain Bushveld: Distributed throughout much of the low-lying and elevated areas within the mountain range, this vegetation community consists of a mixture between mosaic open and closed woodlands, bushveld environments, and moist thickets that vary significantly with topography.

2. Soutpansberg Mistbelt Forest: Primarily located within gorges and at the base of vertical cliffs on the southern slopes of the mountain range, this habitat type primarily comprises of tree species including *Podocarpus latifolius, Xymalos monospora,* and *Podocarpus falcatus* (Mucina and Rutherford, 2006).

3. Soutpansberg Summit Sourveld: restricted to altitudes approximately 1200 m above sea level, this vegetation type is characterised by east-west facing slopes and is abundant with rocky outcrops, and medium-sized shrubs like *Coleochloa setifera* and *Maytenus acuminate* (Mucina and Rutherford, 2006).

4. Makhado Sweet Bushveld: Primarily occurring on the low-lying plains south of the Soutpansberg Mountains, this vegetation type primarily consists of a mixed scrubby woodland and shrubby bushveld environment. Similarly, this vegetation type is characterised by the high presence of small-scale agricultural activities, cattle grazing and private game and hunting farms (Mucina and Rutherford, 2006).

5. Musina Mopane Bushveld: Distributed north of the Soutpansberg Mountains and south of the Limpopo River, this area has a rolling terrain and consists of mixed open- and closed-shrublands and open savanna. Plant communities found in the shrublands include *Colophospermum mopane* and *Terminalia prunioides*, whereas *Terminalia sericea, Grewia flava,* and *Colophospermum mopane* dominate the savanna habitats (Mucina and Rutherford, 2006).

2.2.5 Fauna

The Soutpansberg Mountains are considered to be a 'biodiversity hotspot' and contain roughly 59.9% of South Africa's mammals, (Gaigher and Stuart, 2003), 76% of the country's non-oceanic birds (Berger *et al.*, 2003) and 36% reptile species (Berger *et al.*, 2003). Similarly, Lake Fundudzi in the northwest section of the mountains is home to approximately 28% of all of South Africa's freshwater fish species (Berger *et al.*, 2003)

Invertebrates in Soutpansberg include up to 309 species of butterfly, 52 species of dragonflies and a diverse range of ant species (Munyai *et al.*, 2015). Similarly, the Soutpansberg Mountains are considered to be an arachnid hotspot, with over 23 species of scorpions (Foord, Gelebe and Prendini, 2015) as well as 337 spider species in the 50 km^2 surrounding Lajuma alone (compared to 139 species found in Kruger) (Foord *et al.*, 2008)

There are twenty-five species of non-domesticated ungulates present in the Soutpansberg, with relatively common species like bushbuck (*Tragelaphus scriptus*), bushpig (*Potamocherus larvatus*), warthog (*Phacochoerus aethiopicus*), red duiker (*Cephalopus natalensis*), mountain reedbuck (*Redunca fulvorufula*), common duiker (*Silvicapra grimmia*), eland (*Taurotragus oryx*), and klipspringer (*Oreotragus oreotragus*) (Chase Grey, 2011). There are several species that are now restricted to either private game farms or protected areas after being locally exterminated (Chase Grey, 2011). These include sable antelope (*Hippotragus niger*), white rhinoceros, plains zebra (*Equus quagga*), buffalo (*Syncerus caffer*) and nylala (*Tragelaphus angasii*). As a result of the localised extinction of these ungulates and other large herbivores such as elephants (*Loxodonta africana*) and black rhinoceros (*Dicero bicornis*), much of the grasslands surrounding Soutpansberg have been replaced by secondary bush encroachments (Hahn, 2006).

Despite being surrounded by agricultural areas and human settlements, the Soutpansberg Mountains are home to an assortment of carnivore taxa. Mesocarnivores present include aardwolf (*Proteles cristatus*), common genet (*Genetta genetta*), the African civet (*Civettictis civetta*), the African clawless otter (*Aonyx capensis*), caracal (*Felis caracal*), honey badger (*Mellivora*

capensis), serval (*Leptailurus serval*) and four species of mongoose (*Atilax paludinosus*, *Helogale parvula*, *Galerella sanguinea* and *Mungos mungo*) (Chase Grey, 2011). As cheetahs (*Acinonyx jubatus*) and lions (*Panthera leo*) have been eradicated from the mountains, although the former are sometimes seen, the only two large carnivores resident in the mountains are brown hyaenas (*Hyaena brunnea*) and African leopards. Although it seems likely that a secretive nature combined with a generalist diet allowed for the persistence of these two species throughout the mountain range, both suffer from local persecution as a result of being perceived as threatening to both livestock and private game stock (Chase Grey, 2011; Williams, 2017). Finally, both African wild dogs (*Lycaon pictus)* and spotted hyaenas (*Crocuta crocuta*) are occasionally captured on Primate Predator Project (PPP), yet it is not known how common these animals are in the region (Chase Grey, 2011).

The Soutpansberg Mountains contain all five non-human primate species found in South Africa, with chacma baboons , samango monkeys (*Cercopithecus albogularis schwarzi*), vervet monkeys(*Chlorocebus pygerythrus*), thick tailed bush babies (*Otolemur crassicaudatus*) and lesser tailed bush babies (*Galago moholi*) (Chase Grey, 2011). Known primate predators in the Soutpansberg are the rock python (*Python sebae natalensis*) (Willems, 2007; Tomlin, 2016), leopards and several species of eagle (crowned and Verreaux's) (Willems, 2007; Coleman, 2013; Tomlin, 2016).

2.2.6 Human Communities and Land Use

The Soutpansberg Mountains, as well as the surrounding low-lying areas, are located in the Makhado Local Municipality (MLM). At roughly 8,300 km^2, the MLM contains five large towns (Makhado, Vleifontein, Vuwani, Waterval and Dzanani) and approximately 279 rural villages (Tshilidzi Madzivhandila, Sibanda and Gwelo, 2016). The closest community to the study site is Buisdorp (Buysdorp), a village located on the south-western periphery of the mountain range with a total population, as of 2011, of 629 individuals (Statistics South Africa, 2011). 14 km away from Buisdorp is the mining town of Vivo, located in the Blouberg Local Municipality, which lies directly west of the Soutpansberg Mountains (Statistics South Africa, 2011).

A 2011 demographic census states that MLM has a population of approximately 516,036 individuals (Statistics South Africa, 2011) that has been steadily rising since 1996. It is expected that, by 2020, the population in the MLM will increase to an estimated 561,343 individuals (Statistics South Africa, 2011). 97.3% of people residing in the MLM identify as black African, whereas the remainder of the population in the municipality identify as being Indian/Asian (0.4%), coloured (0.2%) and White (2.0%) (Statistics South Africa, 2011). Tshivenda is the most common language spoken in the municipality (67.3%), followed by Xitsonga (21.9%), Sepedi (2.6%), Afrikaans (2.2%) and English (1.2%) (Statistics South Africa, 2011).

The Western Soutpansberg Mountains is comprised of numerous property and land use types, such as community and private cattle farms, agricultural areas, recreational sites, game ranches, ecotourism zones and conservation preserves (Chase Grey, 2011). While the vast majority of the land in the western Soutpansberg is owned by Afrikaners who utilise properties for cattle ranching and recreational use, the local Venda and Buys communities primarily engage in commercial and subsistence livestock (Chase Grey, 2011). Estates dedicated ecotourism or game hunting are owned and managed by British South Africans (Chase Grey, 2011). Due to a combination of legislative changes and decreased profitability, many of the cattle farms found within and around the western Soutpansberg have been converted to game ranches (Chase Grey, 2011).

2.3 Focal Populations

2.3.1 Leopards in Western Soutpansberg

Leopards have been formally monitored in the western Soutpansberg since 2006, with a permanent array of camera traps for monitoring large predators and other local wildlife established in 2011 as part of the Primate & Predator Project (PPP). The project's primary objectives encompass assessing the behavioural ecology of primate and large predator species within the area (including predator-prey interactions), determining the viability of the western Soutpansberg Mountains as a location for conservation and attaining a greater understanding of local human-wildlife interactions. As the largest carnivore in the area, leopards have been closely monitored by PPP staff and researchers

through scat analysis, camera trapping and telemetry data (through GPS collars) as a means to assess their diet, activity patterns, distribution and population dynamics throughout the mountain range (Chase Grey, 2011; Grey, Kent and Hill, 2013; Fitzgerald, 2015; Chase Grey, Bell and Hill, 2017; Williams *et al.*, 2017).

A previous analysis with the utilisation of camera traps determined that leopards in western Soutpansberg are active throughout the 24-hour cycle, and, within this time span, they are most active during the night and least active at midday (L. Fitzgerald, 2015). Fitzgerald (2015) suggested that these activity patterns reflect optimal time periods for leopards in the western Soutpansberg to hunt, given that their primary prey are also active at such times.

There have been several studies of the feeding ecology of leopards in the western Soutpansberg (Power, 2002; Schwarz and Fischer, 2006; Fitzgerald, 2015; Chase Grey, Bell and Hill, 2017). While the total number of species being consumed has differed between analyses (13 species in Schwarz and Fischer 2006; 22 species in Fitzgerald 2015; 10 species in Chase Grey *et al.,* 2017 and 28 species in Williams *et al.*, 2018), all studies complement a previous meta-analysis conducted by Hayward (*et al.,* 2006), suggesting that leopards have a dietary preference for small- to medium-sized prey.

Species like the bushbuck, common duiker, members of Hyracoidea (hyrax) and vervet monkey seem to be of relative importance as the preferred prey of leopards in the western Soutpansberg Mountains (Table 2.1) (Chase Grey, Bell and Hill, 2017).

Table 2.1 Results from the most recent dietary analysis (through relative frequency of occurrence and relative biomass consumed) for leopards in the Western Soutpansberg recorded by (Chase Grey, Bell and Hill, 2017).

Species	**Relative frequency of Occurrence (%)**	**Relative biomass consumed (%)**
Bushbuck *(Tragelaphus scriptus)*	42.9	49.6
Hyrax *(Procavia capensis)*	26.0	21.3
Vervet Monkey *(Chlorocebus pygerythrus)*	10.4	8.63
Porcupine *(Hystrix cristata)*	5.2	5.12
Common Duiker *(Sylvicapra grimmia)*	5.2	5.49
Chacma Baboon *(Papio ursinus)*	4.2	4.14
Red Duiker *(Cephalopus natalensis)*	3.1	2.91
Mountain Reedbuck *(Redunca fulvorufula)*	1	1.16
Kudu calf *(Tragelaphus strepsiceros)*	1	0.86
Thick-tailed Bushbaby *(Otolemur crassicaudatus)*	1	0.79

While an initial analysis concluded that the Soutpansberg Mountains had the highest population density of leopards outside of any protected area in South Africa, at approximately 10.7 adult individuals per 100 km^2 (Chase Grey, Kent and Hill, 2013), recent findings suggest that the population has crashed dramatically to 6.55 individuals in 2012 and 3.65 individuals per km^2 as of 2016 (Williams *et al.*, 2017). At that rate of decline it was extrapolated that the

leopard population within the western Soutpansberg Mountains would become extinct by 2020 (Williams *et al.*, 2017). It was suspected that such a rapid decline is most likely due to a combination of factors, such as isolation from immigration due to the confined boundaries of suitable leopard habitats being surrounded by anthropogenic habitats (Chapter 3), as well as direct human persecution from snaring, poisoning and shooting (Williams *et al.*, 2017).

2.3.2 Baboons in Western Soutpansberg

Baboons in the western Soutpansberg began to be monitored in 2002, when Tom Larimer spent two years (2002-2004) habituating one group (hereon known as 'House Troop') residing in proximity to the Lajuma property. Following this, House Troop were studied intermittently by both students, primate research coordinators and assistants (De Raad, 2012; Howlett *et al.*, 2014; Tomlin, 2016). After a period of absence from human observers, House Troop were re-habituated in 2011. Continuous monitoring and data collection for House Troop through focal and scan sampling began in early 2014 with the aid of a primate research coordinator and volunteers. Female baboons (N= 3) were equipped with GPS collars between 2013 and 2015. In 2011, the troop's size ranged from approximately 70 to 80 individuals (Tomlin, 2016), but it is believed that this number has increased to around 90 since (Allan *personal communication*).

Baboons in the western Soutpansberg primarily feed on fruits, seeds, leaves and grasses from over 40 species of plants (Appendix 1; Table S1.1) but also eat a variety of animal material ranging from insects and eggs to younger and smaller antelope (bushbuck, red duiker and common duiker), crested guinea fowl (*Guttera pucherani*) and lagomorphs (Tomlin, 2016). Furthermore, baboons in western Soutpansberg have predated upon vervet monkeys (Willems, 2007). Baboons in Soutpansberg tend to sleep on vertical south-oriented sleeping cliffs at night rather than trees, a practice that may provide protection against both the elements and leopards. So far, researchers have recorded that 17 sleeping sites utilised by the habituated troop, with the majority of sites being within their core home range. Seasonality may act as a limiting factor for baboons in the western

Soutpansberg, as they have altered their daily travel distances in both winter and summer, possibly as a response to food availability (De Raad, 2012).

2.3.3 Predation on Baboons

Leopards are the only predator throughout the study site that poses a threat to adult baboons, yet several raptor species, as well as African rock pythons, have the potential to not only elicit alarm calls, but also predate on young individuals. Since being habituated, several instances of predation and attempted predation events have been witnessed by previous researchers and assistants. For example, Tomlin (2016) reports the death of a juvenile after sustaining injuries from a python attack and witnesses an infant succumb to a failed raptor attack within the same year.

Previous scat analyses have shown that baboons in the western Soutpansberg are occasionally predated on by leopards with a relative frequency of occurrence found in scats ranging from 4.2% (Chase Grey, Bell and Hill, 2017), 6.5% (Fitzgerald, 2015) and 6.7% (Schwarz and Fischer, 2006). Since being habituated there have also been several interactions between leopards and baboons recorded by PPP researchers and assistants. For example, in 2014, a primate research coordinator witnessed a failed predation event that eventually led to the death of an adult male (Howlett *personal communication).* In this instance, the male was mortally wounded in a highly vegetated area near the bottom of a southern oriented facing cliff at around 14:00 LMT. Following the attack, the leopard (possibly an adult male) quickly dispersed after being mobbed by the remaining troop members.

Similarly, Allan (*personal communication*) witnessed several diurnal encounters between the habituated group and unknown leopards (Allan, *personal communication*). All of these instances occurred in grassy areas, within close proximity to a sleeping site, and resulted in the baboons loudly barking or 'wahooing' while retreating to the safety of a nearby cliff. While not a direct encounter, Tomlin (2016) reported three adult females that went missing at night on or near sleeping sites. These instances may have been due to successful predation events.

Radio-collared leopards have proximity loggers attached that interact with those of proximity-collared baboons in both baboon groups under a fixed distance, so it is possible to record encounters without the presence of a human observer. Proximity loggers are designed to record when two (proximity) tagged individuals come into a certain distance from one another. In one instance, a male leopard appeared to have stalked the habituated baboon group around mid-afternoon and within close proximity to a sleeping site (Figure 2.6). However, the data suggest that the baboon group spotted the leopard, as the former quickly dispersed down into the safety of their sleeping cliff, at which point, the leopard appeared to have moved on.

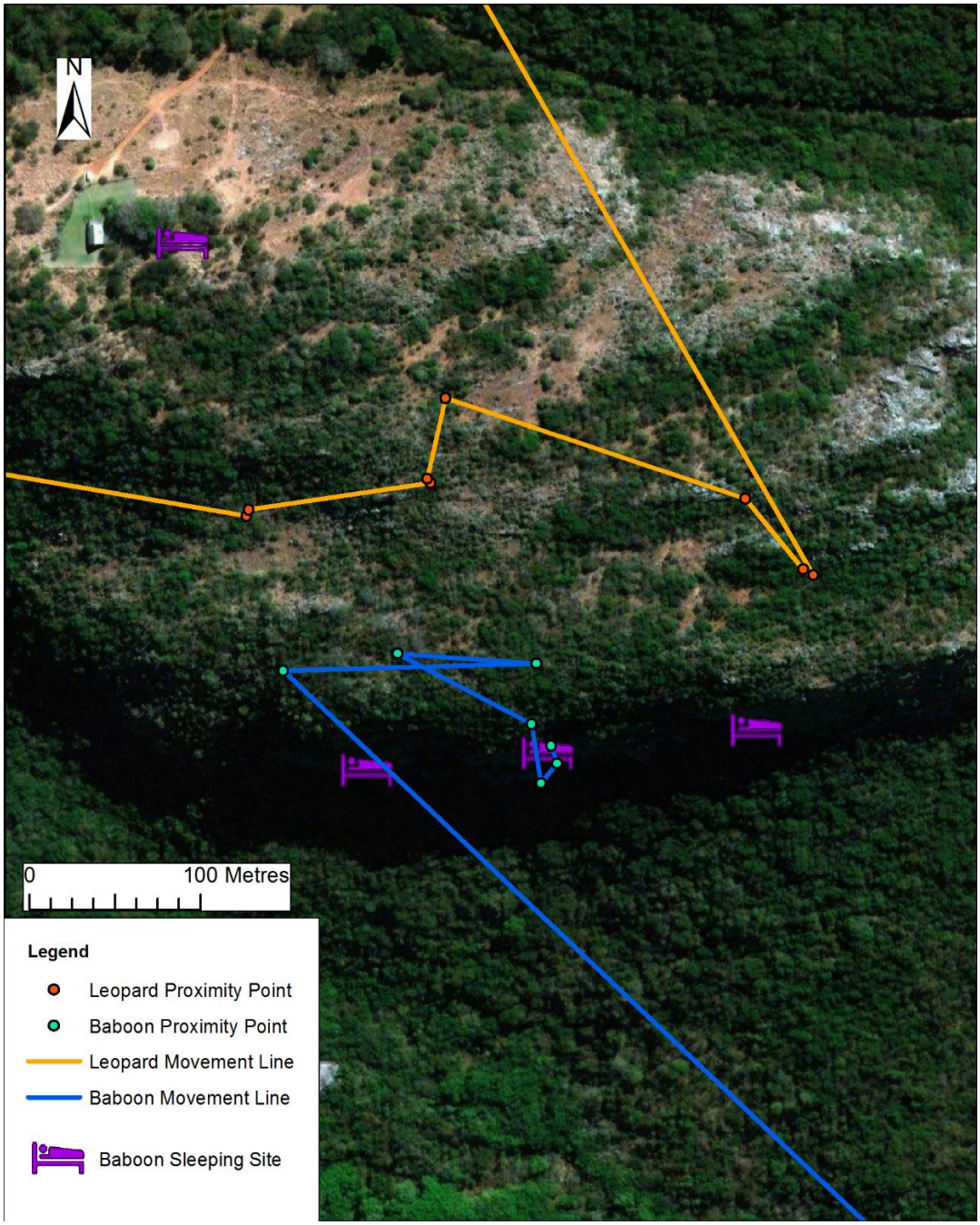

Figure 2.6 Encounter between a male leopard and the baboon troop recorded by GPS collars.

Two predation events occurred on House Troop in 2017. In one instance, a proximity-collared adult female was likely attacked at around 8:00 am on 13 July 2017 near the same sleeping site where the proximity event occurred (Sleeping site 5). The leopard was subsequently scared off, but two days later, a known adult male leopard came back to retrieve the remains in the early morning (see figure 2.7).

Figure 2.7 Camera trap image of adult female baboon being dragged away by an adult male leopard two days after the actual kill event.

Later that year (2 November 2017), an adult male baboon was attacked sometime in the late morning and found dead with puncture marks near his spine and slashes over his body. It was assumed that the leopard responsible fled after being chased away.

2.3.4 Human Communities and Focal Species

Both focal species (leopards and baboons) are mostly viewed negatively by ranchers and farmers (Chase Grey, 2011; Chase Grey, Bell and Hill, 2017; Allan *personal communication*). Local livestock ranchers feel threatened by the presence of leopards due to the latter's ability to predate on cattle, sheep and goats. While leopards in the Soutpansberg have occasionally hunted livestock (Williams *personal communication*), three previous dietary analyses conducted in the western Soutpansperg have found no evidence of livestock in faecal remains (Schwarz and Fischer, 2006; Fitzgerald, 2015; Chase Grey, Bell and Hill, 2017). Additionally, Chase Grey (*et al.,* 2017) indicated that leopards residing on or near properties containing livestock or valuable game such as nyala, sable antelope, and blue wildebeest (*Connochaetes taurinus*) prefer to consume preferred species, such as bushbuck and common duiker, with no evidence of valuable game or livestock found in scat. Therefore, it is likely that the *perceived* threat from leopards by livestock owners is greater than it actually is (Chase Grey, Bell and Hill, 2017). Despite this, the attitudes held by many livestock

ranchers escalate into retaliatory actions as exemplified by the death of an adult male killed (via poisoned bait, Table 2.6) by a landowner who suspected that the cat was predating on his cattle.

However, many local game ranchers tolerate the presence of leopards on their property despite the fact they occasionally predate on game species such as impala, hartebeest (*Alcelaphus buselaphus*), and blue wildebeest (Chase Grey, 2011; Chase Grey, Bell and Hill, 2017). It is likely that this tolerance stems from how leopards may provide monetary gain through either trophy hunting or ecotourism (Chase Grey, Bell and Hill, 2017).

Baboons are often viewed as pests by farmers, as they frequently raid commercial plant crops (Hill, 1997, 2000; Findlay, 2016). In the context of the study site, baboons often raid a macadamia farm located within their home range (Allan, *personal communication*). Due to this, local workers attempt to scare the baboons away, sometimes with little success. As a result, much of the alarm call and vigilance data were collected from within the vicinity of the farm.

2.4 Data Collection

2.4.1 Overview of Fieldwork and Data Collection

This thesis required the analysis of multiple datasets that were collected at different points in time. Given the subject matter of my research, extensive fieldwork was not required and my time spent at the field site lasted only from October to December 2015. Although brief, this time period was vital to my research as it allowed me to attain a crucial understanding of the diverse array of environments found within the western Soutpansberg Mountains and also experience first hand the daily behaviour and travel routes of the habituated focal baboon group. The fieldwork also provided my with direct experience of the other data collection methods on site (e.g. phenology). Due to my limited time in the western Soutpansberg Mountains, specific data collected by myself was limited to leopard kill sites that were used in Chapter 3.

Although full descriptions of the datasets utilised in this study are listed in the subsections below or in their relevant chapter, please see Table 2.2 below for a brief list of datasets used in this study.

Table 2.2 Summary of Primary Datasets Used (PPP = Primate Predator Project).

Dataset	Time Frame	Originally Collected By	Chapter(s)
Leopard GPS Data	2012-2015	PPP	3, 4, 5
Baboon GPS Data	2014-2017	PPP	5
Leopard Accelerometer Data	2012-2015	PPP	4
Baboon Accelerometer Data	2013-2015	PPP	6
Leopard Kill Site Data	2012-2015 (collected in 2015)	Myself	3
Vegetation/Phenological Sampling	2014-2017	PPP	6
Food Availability	2014-2017	Derives from Vegetation/Phenological Sampling but Dataset created by myself.	6
Meteorological Data	Varies by Chapter	Lajuma Research Centre	4,6
Temporal Data	Varies by Chapter	NASA	4,6
NDVI	Varies by Chapter	Landsat	3,4
Topographic Data	Not Applicable	SRTM (Slope and Ruggedness Created by me)	3,4
Waterway Data	Not Applicable	Created by me with the aid of topographic data.	3,4,5
Agricultural Areas	Not Applicable	SANBI	3,4
Buildings	Not Applicable	Created by me with the aid of Google Maps	4

2.4.2 Baboon Behavioural Data

The behavioural data used for analysis in chapter 6 were collected on 'House Troop' by PPP staff members and assistants between 2014 and 2017. The data collected include 30 minute behavioural scans on individual baboons from the time periods during which they depart from and arrive to sleeping sites

throughout the day (Table 2.3 and Table 2.4). GPS coordinates were taken before the beginning of each behavioural scan with the aid of a Garmin GPS device. Activities recorded include events such as feeding (as well as food type being consumed), vigilance, height from the ground (to the nearest metre), nearest neighbours, movement and social behaviours (grooming, aggression, mating, etc). The age, sex and identity of the individual were also recorded if possible. Environmental data recorded at the time of the scan include time of day, categorical habitat types and weather conditions (cloud coverage, precipitation and wind conditions).

Table 2.3 Primary activities recorded by PPP staff through baboon scan samples.

Primary Activity	**Qualifier (Subtype)**	**Description**
Resting	Resting sitting	Individual is stationary while sitting without performing any other activity.
	Resting standing	Individual is stationary while standing without performing any other activity.
	Resting lying	Lying down.
	Resting huddled	Huddling with other individuals.
	Self-grooming	Grooming itself, also referred to as autogrooming.
Feeding	Feeding	Searching for, processing, or ingesting food.
	Foraging	Actively searching for food that is not obvious without ingesting anything.
	Feeding (cheek pouch)	Feeding from food items stored in cheek pouches.
Moving	Walking	Always 3 limbs touching the ground. Also applies to slow climbing.
	Running	Fewer than 3 limbs always touching the ground. Applies to fast climbing.
Socialising	Grooming given	The individual is grooming another individual.
	Grooming received	The individual is being groomed by another individual.
	Play	Individual involved in social play.
	Aggression	Individual involved in an aggressive display as the aggressor.
	Submission	Submissive in an aggressive display.

	Mating	Self-explanatory.
Other	Other	Behaviour not mentioned.
Drinking	Drinking	Self-explanatory.

Table 2.4 Additional behavioural information recorded during scans.

Additional Information	**Description**
Nearest Neighbour	Number of individuals within 5m of the focal individual (does not include dependent infants).
Height from ground	To the nearest meter
Vigilance Subtypes	Not vigilant. Looking upwards. Looking downwards. Scanning in a horizontal plane. Looking at the observer. Social vigilance, looking at another monkey. Other (e.g. looking at a different species). Unknown.

While the data were primarily recorded at 30 minute intervals, primate researchers and assistants also noted spontaneous '*Ad libitum'* events between scans (Table 2.5). Notable '*Ad lib*' events include predation events, interspecific interactions (same site feeding or occasional predation by the baboons), intraspecific encounters between other troops and alarm calling. The locations of all '*Ad lib'* events were recorded with a Garmin GPS device.

Table 2.5 Ad-libitum behaviour recorded between scans.

***Ad-libitum* categories**	**Qualifier (Subtype)**	**Description**
Vocalisation	Alarm call	Self-explanatory.
	Wahoo	Call used in male dominance displays.
	Lost calls	Made when group is separated.
	Other	Any other relevant vocalisation.
Encounter	Inter-specific encounter	The presence of members of another species within 10m of an individual from the troop.
	Within-specific encounter	Interactions with another group. Record all details in the comments section.
Behaviour	Aggression	Aggressive encounters involving more than one individual.
	Mating	Mating (regardless of whether it is in a scan or not).
	Other	Any other interesting behaviour.
Predation	-	Details of any predation event.

2.4.3 GPS Data Collection: Leopards

Between 2012 and 2014, eight leopards (six males and two females) were collared within the study site. After being captured by foot hold traps, leopards were sedated with either Zoletil or a Zoletil/Medetomidine combination by a

South African registered veterinarian. Collaring was approved by the Department of Anthropology ethics committee and the Animal Welfare Ethical Review Board at Durham University. All leopards were fitted with Vectronic GPS-PLUS collars (VECTRONIC, Aerospace, Berlin, Germany) that were programmed to take GPS fixes at 3 hours and 20 minute intervals and were designed to fall off 455 days after the collars were put on. Leopard telemetry data were downloaded regularly through an Ultra High Frequency (UHF) terminal. All leopard collars were designed to take 20 minute GPS fixes when in proximity to baboon proximity collars, although the data from these fixes were not utilised in this study.

Figure 2.8 Adult male leopard wearing a GPS collar.

Unfortunately, only two collared leopards (now monitored through camera traps) remained as of 2017, as the other six either died due to anthropogenic causes or disappeared entirely. While the majority (N=7) of the collared leopards primarily resided on the highly vegetated, southern slope of the mountain range, one male ('Drogo') expanded his home range to the less productive and arid northern side. Home range sizes varied significantly with the largest belonging to the male residing in the far northern part of the

mountain and the smallest belonging to a female living at mountain range's southern-most edge (Chapter 3).

Table 2.6 Collared leopard information.

Collar ID	Name	Date Collared	Sex	Status	Notes
11534	Michel	2012-06-08	M	Deceased	Killed by a snare. Photographs with snare taken on 07/08/13.
10001	Drogo	2012-06-15	M	Deceased	Killed by local rancher. Probable cause of death is poisoned bait. Last Photograph taken on 16/03/13.
10012	CC	2012-07-21	F	Deceased	Killed by a snare in October 2012. Gave birth to BB.
10013	Anni	2013-02-12	M	Unknown	Unknown but suspected dead. Last photo taken on 16/03/2013.
10011	BB	2013-06-12	M	Alive	Alive but not collared. Mother is CC.
10012	Jenny	2013-09-19	F	Alive	Alive but not collared.
12846	O'Malley	2014-04-18	M	Unknown	Unknown but suspected dead. Last photograph taken on 24/06/2014.
10009	Pimms	2014-07-17	M	Deceased	Killed by a snare. Most likely died on 16/06/15.

2.4.4 GPS Data Collection: Baboons

Baboons from two different groups, the habituated 'House Troop' and an unhabituated troop, were collared between the years 2013 and 2015 with Vectronic GPS-PLUS collars (VECTRONIC, Aerospace, Berlin, Germany). Since male baboons would leave their natal group upon reaching adulthood, only adult females were collared. This practice was particularly useful for collecting data on 'House Troop,' as it allowed both for behavioural data to be collected side-by-side with GPS data and for monitoring to occur on days when PPP staff members or assistants were absent. To conserve battery life, collars were primarily programmed to take GPS fixes during the time periods when the baboons were active. As a result, GPS fixes were taken every hour between 04:00 and 18:00 SAST (South African Standard Time) with the exception of one nocturnal fix at 22:00 (in the event that their sleeping site shifted in the middle of the night). Baboon telemetry data were downloaded regularly through an Ultra High Frequency (UHF) terminal. While several individuals were collared with proximity tags that interacted with both leopard and baboon GPS collars, such data were not utilised for any analyses in this thesis. The collaring of baboons was approved by The Department of Anthropology Ethics ~~c~~ committee and the Animal Welfare Ethical Review Board at Durham University.

Figure 2.9 Adult female baboon wearing a GPS collar.

Table 2.7 GPS collared baboon information.

Collar ID	Name	Date Collared	Sex	Group	Status	Notes
11941	Lobelia	09/03/2013	F	Habituated Group (House Troop)	Alive	-
11940	Unhab	06/11/2015	F	Unhabituated Group	Alive	-
11942	Melissa	07/27/2014	F	Habituated Group (House Troop)	Alive	Was pregnant.
11938	Melissa (collared twice)	06/04/2015	F	Habituated Group (House Troop)	Alive	Gave birth to infant in March 2016

2.4.5 Accelerometer Data Collection

Incorporated into both leopard and baboon GPS collars were dual-axis activity sensors that continuously recorded acceleration on two different axes, X and Y (Berger, Dettki and Urbano, 2014). The Y-axis represented sideward and rotary moments, whereas the X-axis recorded forward and backward movements. Activity values were continuously taken every four seconds, averaged and then stored within a range from 0 (no activity) to 255 (high activity). As accelerometers were attached to GPS collars, they were designed to fall off 455 days after being fitted, with data downloaded regularly through an Ultra High Frequency (UHF) terminal.

In the context of this thesis, 'activity' refers to any movement that is recorded, regardless of the animal's position and behavioural state (Scheibe *et al.*, 1998). Although specific behaviours have been found to positively correlate with certain activity levels (for example, high activity levels found in carnivores may reflect subduing prey (Wang, Nickel, Rutishauser, C. Bryce, *et al.*, 2015), it is virtually impossible to attribute specific behaviours to activity levels without observing

every single movement by the animal. Despite this, accelerometers have been proven to be useful for monitoring broad behavioural states and activity patterns in both non-human primates (Sellers and Crompton, 2004; Fehlmann *et al.*, 2017) and carnivores *(*Podolski *et al., 2013;* McClune *et al.,* 2014; Williams *et al.,* 2014).

2.4.6 Meteorological and Temporal Data

All meteorological data utilised in this thesis including wind speed, temperature, and precipitation derived from an SAEON (South African Environmental Observation Network) weather station based on site. In addition, I derived the wind chill equivalent temperature variable (perceived environmental temperature) by combining both the windspeed and temperature variables. All meteorological data were recorded in half hour intervals.

Temporal data including daily sunrise and sunset, day length, astronomical twilight, and lunar luminosity were downloaded from the National Aeronautics and Space Administration (NASA) database (http://aa.usno. navy.mil/). Details regarding the incorporation of such variables can be found in their appropriate chapters (Chapters 4 and 6)

2.4.7 Spatial Environmental Variables

This thesis required the use of spatial environmental data that originally derived from satellite imagery. Using geospatial software (such as ArcGIS) and usually in raster format. Raster files are in a grid format, and typically contain cells (or pixels) of various resolutions that are presented in columns and rows. Rasters deriving from specific satellite imagery (i.e. Landsat) may have colour bands (red, green, blue) found on the electromagnetic spectrum that are used towards interpreting environmental factors such as vegetation productivity. In addition, some raster files may only have one colour band, in which case, often represent a continuous geographical variable (such as elevation). Specific rasters that were utilised or created for this thesis often vary by analysis, and as such, will be discussed in detail in the appropriate chapter.

2.4.8 Vegetation Sampling

Vegetation data utilised in Chapter 5 were collected through quadrat sampling between the years 2014 and 2017 by both PPP staff and assistants. Quadrat samples were at randomly generated points distributed throughout the study site that overlapped with the ranges for all three diurnal primate species (vervet monkeys, samango monkeys, and chacma baboons). Vegetation sampling at these random points was from 5m x 5m quadrats, with data recorded including tree species, number of saplings, percentage of land cover, visibility slope, aspect, as well as canopy cover. DBH (diameter at breast height), height, and crown diameter measurements were collected for all identifiable tree species. These data were used to assess the availability and distribution of fruit bearing tree species throughout the baboons' range.

2.4.9 Phenological Sampling

Phenological data derived from trees that were important food sources for diurnal primate species were tagged and monitored on a monthly basis by PPP staff and assistants in order to assess monthly, seasonal, as well as annual trends in growth and food availability. Data collected by PPP staff include the number of fruits or seeds (when applicable), percentage of unripe fruit, number of leaves and branches, as well as number of flowers per tree. These were used to assess food availability per tree and tree species for baboons.

2.4.10 Food Availability

Following the inspection and organisation of both phenology and quadrat data, I assessed the scan data collected by PPP staff in order to determine the average amount of food items consumed by baboons per month during the study period (Chapter 5). By doing so, I was able to assess both annual as well as seasonal dietary trends, while simultaneously accounting for species that were not consumed during certain time periods. Given that the baboons consumed a large variety of food items throughout the year (Appendix 1; Table S1.1), I decided to only include tree species that constituted the top 5% of the total diet. This was to ensure that species that were rarely consumed were not included in the overall analysis, and thus prevented the inflation of food availability throughout the study site.

It is important to bear in mind that some individual trees recorded in both the phenology and quadratic data did not have fruit or seeds. To account for this, a simple linear regression was used in order to determine if there was a correlation between either DBH, crown or tree height and average fruit availability for each tree species(Coleman, 2013). In the end, crown height was deemed to be the most significant predictor for determining if a tree species bore fruit and seeds and as such, scatter plots were created as a means to visually assess a taxon specific cut-off point. Trees that fell below these cut-off points were assigned a zero (no available fruit) when fruit availability was applied across all habitats.

Important food bearing trees were averaged annually (throughout the study period) or seasonally. Following, the diameters for each seed or fruit were obtained from (Palgrave, 1996) and the volume of an ellipsoid was used as a means to determine total food volume per species through the following formula:

$$V = \frac{4}{3}\pi\, r^3$$

V signifies volume whereas r^3 represents the fruit diameters raised to the power of three. The formula used for flowers characterised the volume for a half ellipsoid:

$$V = \frac{2}{3}\pi\, r^3$$

Fruit and flower availability across taxa were calculated by multiplying the total volume of fruit by the average number of annual or seasonal fruit (or flowers) (Coleman, 2013). In contrast, seed availability was obtained by multiplying the average volume per seed pod (seed volume multiplied by the average number of seeds per pod) by the overall average number of seeds per taxon.

Food availability data for consumed species were then attached to the corresponding tree species derived from the quadrat data. All tree species within the the 5 x 5 metre radius quads that did not constitute in the 5% of total diet as well as individuals below the threshold assigned earlier were given a

value of zero. Following, all trees found within the quadrats were summed as a means to obtain total food availability per quadrat.

All quadrat points that were assigned food values were merged with habitat types deriving from a categorical land coverage map of South Africa created by GeoTerraImage Company (South Africa) accessed through the South African Spatial Data Infrastructure (Dept. of Rural Development and Land Reform, Republic of South Africa) website at http://www.sasdi.net/) that covers the entirety of South Africa (including the western Soutpansberg Mountains). Created through a composite of over 600 Landsat 8 multi-spectral and multi-seasonal images, this raster was chosen for the creation of a categorical food availability habitat map due to its ability to provide a comprehensive classification of habitat types ranging from grasslands, forests, bare earth, as well as anthropogenic land types including agricultural areas at a 30 metre resolution. Finally, both annual and seasonal food availability for the entirety of the study area were obtained by averaging all quadratic points found within each habitat category.

2.5 Statistics

As statistical analyses differ between objectives, all methods regarding data compilation, management and analyses are described in their relevant chapters.

2.6 Software

Primary software utilised include ArcGIS Desktop version 10.3.1 (ESRI, 2014), QGIS Desktop 2.18.15 (QGIS Development Team, 2015), R Studio version 3.4.3 (RStudio Team, 2016), Microsoft Excel (Katz, 2010), Geospatial Modelling Environment (GME) version 0.7.4.0 (Beyer, 2012), Geoda (Anselin, Syabri and Kho, 2006), Google Earth Pro 7.3.1 (Wuthrich, 2006), SAM (Spatial Analysis in Macroecology) version 4.0 (Rangel, Diniz-Filho and Bini, 2010), and Garmin Basecamp (Garmin Inc., 2005). Several software packages and toolboxes were utilised for different analyses and will be listed within the methodology section of the appropriate chapter.

Chapter 3: Leopard (*Panthera pardus*) Habitat Selection and Home Range Utilisation in a Montane Environment

Abstract

Animals often disproportionally utilise specific habitats within their environment as a means to fulfil fitness enhancing opportunities such as resource acquisition. Animals must choose not only where to reside, yet also how they use specific habitats within their home range. With the aid of Resource Selection Functions, I assessed where leopards were likely to establish home ranges within the western Soutpansberg Mountains, South Africa. I also determined where leopards were more likely to spend time within their home ranges, as well as where they are more likely to kill and consume prey. My results showed that although the majority of the western Soutpansberg can be considered suitable habitat, leopards choose to establish home ranges within the mountains and away from anthropogenic habitats in the low-lying areas. In addition, leopards chose to spend time in areas within their home range that were not only a greater distance away from human settlements, but also had greater vegetation productivity, a likely proxy for prey density. Finally, leopards appeared to hunt in proportion to their home range use, suggesting that the areas used by leopards are generally suitable for hunting and consuming prey. Coupled together, these results show that the preservation of preferred habitats should be considered a top priority towards conserving a dwindling population.

3.1 Introduction

Habitat loss and fragmentation due to anthropogenic factors are considered serious threats towards the sustainability of large carnivore populations on a global level (Woodroffe, 2000; William J. Ripple *et al.*, 2014). As human populations increase and penetrate into previously unaltered ecosystems, large carnivores become inherently more susceptible towards localised or regional extinction compared to other mammals due to increased anthropogenic factors as well as a reduction of primary prey (Fuller and Sievert, 2001; Crooks, 2002;

Brashares, 2003; Carbone, Pettorelli and Stephens, 2011). This vulnerability towards extinction enhanced due to large carnivores often having large home ranges, low population densities, slow reproductive rates, and demanding metabolic requirements that come with having a large body size combined with pursuing and subduing prey (Gittleman and Purvis, 1998; Purvis *et al.*, 2000; Carbone, Teacher and Rowcliffe, 2007).

Leopards *(Panthera pardus)* are the most widespread large felid with a geographical range extending from southern Africa, across the Middle East, and into East Asia (Sunquist and Sunquist, 2002). The wide geographical and dietary range of leopards may partially be due to their ability to adapt to an assortment of different environments ranging from deserts, alpine forests, and tropical rainforests (Nowell and Jackson, 1996).

The catholic diet of leopards allows them to hunt both large and small game, although Hayward and colleagues (2006) found that leopards primarily prefer small-medium ungulates ranging between 10-40 kg. Despite their behavioural flexibility, leopard populations have been decreasing at a rate comparable with other large felids (Ripple *et al.*, 2014) and a recent meta-analysis suggested that current leopard populations occupy only 25% of their historical (circa 1750) range (Jacobson *et al.*, 2016). Given these declines the International Union for the Conservation of Nature (IUCN) have reclassified the status of *P. pardus* as vulnerable from near threatened (Stein *et al.*, 2016).

Like many other large carnivore species, human persecution (Balme, Slotow and Hunter, 2009), habitat loss and fragmentation (Balme, Slotow and Hunter, 2010; Swanepoel *et al.*, 2013) as well as loss of primary food sources (i.e. prey) (Henschel *et al.*, 2011) appear to be primary explanations for either the decrease or localised extinction of leopard populations across the globe (William J. Ripple *et al.*, 2014). Habitat loss is particularly dramatic in non-protected areas of South Africa, where human encroachment due to farming has often led to unsuitable, patchy habitats while simultaneously increasing the probability for human-wildlife conflict (Swanepoel *et al.*, 2013, 2015).

Despite 68% of suitable leopard habitat in South Africa occurring in unprotected areas (Swanepoel *et al.*, 2013), there have been few studies that assessed leopard habitat selection and utilisation outside protected areas (although see Balme, Slotow and Hunter, 2010). Additionally, the majority of studies on leopard behavioural ecology (including habitat use) in South Africa have been restricted to woodland or savannah environments (Bailey 1993; Balme *et al.,* 2007; Hayward and Slotow 2009; although see Pitman *et al.,* 2013). Natural refugia such as mountains can often act as barriers that have the potential to restrict agricultural and urban development, and thus, allow carnivore species to persist in areas where human development is in relatively close proximity at lower elevations (Chase Grey *et al.,* 2013). However, several studies have shown that although animals can persist in protected areas this does not necessarily mean that they are optimal for fitness (Noss *et al.*, 1996) nor for the localised survival of the species (Novaro, Funes and Walker, 2005).

Pitman and colleagues (2013) showed that female leopards living in the Waterburg Mountains (South Africa) were highly selective in habitat choice which was associated with the presence of larger carnivore species such as (*Panthera leo*); leopards preferred to hunt and rest in relatively rugged areas where inter-specific encounters were less likely to occur (Ross T. Pitman *et al.*, 2013). These leopards also preferred to predate on high-risk species such as chacma baboons (*Papio ursinus*) which may have been a result of the same ecological pressures (Jooste *et al.*, 2013; Ross T. Pitman *et al.*, 2013).

Where and how species select specific resources across their biogeographical range is important to understanding animal behavioural ecology (Manly *et al.*, 2002; Chetkiewicz and Boyce, 2009). Understanding the key environmental variables and preferred habitats that promote fitness is important in conservation strategies based on habitat preservation and supporting species viability (Manly *et al.*, 2002). Resource Selection Functions (RSFs) are a habitat suitability index that are enhanced through the use of comprehensive datasets as well as logistic regression (Boyce *et al.*, 2002). RSFs are employed to characterise and predict where animals are likely to utilise their environments at different spatial scales (Manly *et al.*, 2002; Boyce *et al.*, 2003).

While animals will disproportionately select specific resources within their environment as a means to enhance fitness (Manly *et al.*, 2002), it should also be noted that resource selection in itself is spatially hierarchal and not uniform throughout time and space (Owen, 1972; Johnson, 1980). Thus, species will first select to range in a specific geographical region (1st order habitat selection) (Wiens, 1973; Johnson, 1980). Following this, individuals will select specific areas (i.e. home range) to live within that range (2nd order selection) and then will disproportionally utilise parts (i.e. patches) of that specific home range for living in (3rd order) and feeding in (4th order) (Johnson, 1980). Avoidance of factors that pose the greatest threat to limiting fitness should be stronger at larger scales (such as selection of home ranges) whereas factors that pose lesser threats towards fitness should be influential at smaller scales (i.e. within home ranges and feeding patches) (Rettie and Messier, 2000). For example, McLoughlin and colleagues (2002) provided evidence that food availability is the primary factor for grizzly bear (*Ursus arctos*) home range selection in the central Canadian arctic whereas both intraspecific predation and foraging habitats are decisive limiting factors within their home ranges.

Very little research has assessed how leopards select specific environmental variables in montane environments in the absence of other large carnivores. This is particularly important in the context of the Soutpansberg Mountains, where the leopard population appears to be in significant decline (Williams *et al.*, 2017), despite the area previously supporting one of the highest densities reported outside of a state-protected area (Chase Grey, Kent and Hill, 2013). This research utilises RSFs to determine if leopards in a montane environment prefer specific environmental variables at different spatial scales.

Landscape attributes were predicted to have an impact on leopard resource selection functions at different scales. Many species (including leopards) select or avoid specific features in the landscape that have the potential to either promote or inhibit fitness (Dickson, Jenness and Beier, 2005; Gavashelishvili and Lukarevskiy, 2008; Simcharoen *et al.*, 2008; Fattebert *et al.*, 2015). Although habitat selection in large, solitary felids has been found to vary between species, several studies have shown that they often prefer to reside or

utilise areas that exhibit sufficient vegetation coverage (Balme, Hunter and Slotow, 2007; Pitman *et al.*, 2013), and are topographically complex such as ruggedness; (Zeller *et al.*, 2017) and slope (Chundawat, 1990; Monroy-Vilchis *et al.*, 2009; Hebblewhite *et al.*, 2011), and are closer to water sources (Simcharoen *et al.*, 2008). Such areas have the potential to provide not only sufficient hunting coverage(Marcella, 2004; Balme, Hunter and Slotow, 2007), yet may also act as refuges from humans or other predators (Zarco-González *et al.*, 2009; Pitman *et al.*, 2013).

In contrast, many felids have been shown to actively avoid human settlements (Ngoprasert, Lynam and Gale, 2007; Zarco-González *et al.*, 2009; Zeller *et al.*, 2017) and agricultural areas (Dickson and Beier, 2002; Zeller *et al.*, 2017). Given these findings, vegetation coverage (through Normalised Difference Vegetation Index), slope, distance from human settlements, agricultural areas, water sources and surface ruggedness were used as predictor variables for leopard habitat use. Aspect was also included as a predictor due to an increase in vegetation coverage on the southern slope (Mucina and Rutherford, 2006). Finally, elevation was added as a predictor variable since highly elevated areas (on the mountains) are not only more topographically complex yet contain a greater abundance of natural habitats.

The primary objectives for this analysis were to assess leopard resource selection functions within western Soutpansberg on three hierarchal spatial scales. This includes assessing environmental and anthropogenic factors that may impact leopard home range selection within the western Soutpansberg Mountains (2nd order), how home ranges are utilised due to such factors (3rd order), as well as where leopards choose to hunt within their home ranges (4th order).

It is anticipated that leopards in western Soutpansberg will be highly selective towards environmental variables that are characteristic of the mountain range on all scales; it is also expected that the significance of these variables will decrease as they become more prevalent within smaller spatial scales (i.e. 3rd and 4th order). While Soutpansberg may provide suitable habitat for leopards (Chase-Grey *et al.,* 2013), a recent analysis by Williams (*et al.,* 2017) permits an

expectation that human presence as well as persecution (such as trapping or hunting) act as the most limiting factors for leopard habitat suitability.

3.2 Methods

3.2.1 Study Site

This study was conducted in the western Soutpansberg Mountains (Limpopo Province, South Africa) (23°06'45.14"S 29°11'37.10"E). Categorised by a topographically complex Afro-Montane environment, the western Soutpansberg is part of the Vhembe Biosphere Reserve (UNESCO), and area recognised for its biodiversity as well as the presence of numerous endemic species found within the region (Van Wyk & Smith 2001; VBR 2012) (Section 2.2).

3.2.2 Leopard Collaring Methods

Eight adult leopards (six males and two females) were captured with foot snares between June 2012 and July 2014 and fitted with Vectronic GPS-PLUS collars (VECTRONIC, Aerospace, Berlin, Germany). Captured leopards were sedated with either Zoletil or Zoletil/Medetomidine combination and by a South African registered veterinarian before being fitted with collars. All collars were programmed to take GPS fixes every 3 hours and 20 minutes and were designed to fall off 455 days after collars were deployed, with a UHF device used to download data at regular intervals (Section 2.4.3).

3.2.3 Environmental Variables

Topographic data (slope, aspect, elevation, ruggedness) were derived from a 30 meter resolution digital elevation model (DEM) provided by the Shuttle Radar Topography Mission (SRTM), downloaded from the United States Geological Survey (USGS) Earthexplorer website (http://earthexplorer.usgs.gov/). Slope and aspect were created in ArcGIS 10.3.1. (Environmental Systems Research Institute, Inc., Redlands, CA, USA) through the slope and aspect tools in the Spatial Analysist toolbox. Waterway data were derived through the aid of the Optimized Pit Removal Tool extension (Center for Research in Water Sources, Austin, TX) for ArcGIS. Ruggedness, being defined as a landscape characteristic that exhibits steep and irregular terrain (Sappington *et al.,* 2007) has been shown to be an important predictor variable for leopards (Edgaonkar, 2008; Swanepoel *et al.*, 2013) and was therefore included in this analysis. A

ruggedness layer was created through the Benthic Terrain Modeller toolbox for ArcGIS (Rinehart *et al.*, 2004).

Six Monthly Landsat-8 Operational Land Imager (OLI) and Thermal Infrared Sensor (TIRS) images (30 metre resolution) taken from July, October, November 2013 and April, June, August 2014 were downloaded from the USGS Earthexplorer website to create an NDVI composite. These dates covered the time when the majority of the animals were collared and are seasonally divided between wet and dry. NDVI was calculated for each individual month using the following equation (Cabral, Freitas and Fiszon, 2007):

$$NDVI_n = \frac{IR_n - R_n}{IR_n + R_n}$$

Where IR(infrared) represents the 5th spectral band whereas R(red) represents the 4th spectral band. Monthly NDVI images were composed with the use of the Image Analysis function in ArcGIS.

Normalised Difference Vegetation Index (NDVI) serves as an index of both primary productivity as well as vegetation structure (Myneni *et al.*, 1995) and has been useful in research ranging from movement studies to wildlife management (Pettorelli *et al.*, 2011). Specifically, NDVI has also been in carnivore research and felid habitat selection (Erfanian *et al.*, 2013; García-Rangel and Pettorelli, 2013).

In addition to NDVI, A categorical (vector) habitat map (Vegmap, South African National Biodiversity Institutes) was initially used for this analysis and derived from the SANBI website (http://bgis.sanbi.org/) (Chapter 2, Section 2.24 for habitat descriptions; Appendix 1, Figure S1.1 for visual projection).

To compare categorical habitats and NDVI, 50 points were generated in each available habitat (n=6) found in buffered leopard home ranges. A Kruskal-Wallis test was performed with the results displaying that there were significant differences found between NDVI values (and thus, the amount of vegetation) and habitat type ($x^2(2)$= (188.773),df =5, p=<0.0001). A post hoc pairwise comparisons showed that out of 15 pairwise comparisons, 9 were significantly different (p=<0.0001).

Urban and agricultural rasters were obtained from The South African National Land Cover Map derived from the SANBI website (http://bgis.sanbi.org/DEA_Landcover/project.asp) which were derived from Landsat-8 imagery at a 30 metre resolution. Urban and agricultural areas were isolated and converted into vector format through ArcGIS. Euclidean distances from all leopard GPS locations were derived from the Euclidean Distance function within ArcGIS.

3.2.4 Second Order Resource Selection Functions

For second order resource selection functions, I assessed whether leopards specifically chose or avoided available areas within the study site to establish home ranges. A used/available design was employed where leopard (used) GPS points were compared with an equal number of random (available) samples (n=7679) (Manly *et al.*, 2002).

Since the collared leopards had unequal numbers of GPS fixes, I constrained the sampling area for second order resource selection to 3km buffers surrounding 99% isopleths derived from kernel density estimates from individual leopard home ranges through Geospatial Modelling Environment (GME ;Beyer 2012; R Development Core Team 2012). Buffers constituted the smallest known size of a female leopard's home range (Grassman, 1999), thus depicting areas theoretically available to each animal. This method allows for the inclusion of all available leopard data while simultaneously permitting control for variable sample sizes.

Random (available) points that were equal in total to each individual leopard's (use) GPS fixes were generated through GME and distributed throughout buffered areas in ArcGIS as a means to achieve a 1:1 ratio (Koper and Manseau, 2012).

All environmental predictor variables were projected into ArcGIS along with each individual's buffered range, and all used/available data. All environmental predictor variables were spatially joined with each corresponding points and were subsequently extracted from ArcGIS for analysis.

3.2.5 Third Order Resource Selection Function and Home Range Analysis

The third order RSF had a used/available design where leopard GPS fixes (used) were compared to an equal number of randomly generated points (available) from within the home ranges of each individual animal (Manly *et al.*, 2002). 95% home ranges for each leopard were generated through fixed Gaussian Kernel Density Estimates (KDE) in Geospatial Modelling Environment. 95% KDEs were chosen for this analysis as a means to control for exploratory behaviour outside of the main ranging area (Majumder *et al.*, 2012). The Least Squared Cross Validation bandwidth (LSCV) was used as a smoothing parameter given that such a bandwidth showed minimal discrepancies when combined with fixed KDEs (Erran Seaman and Powell, 1996; Simcharoen *et al.*, 2008).

Random (available) samples were generated through Geospatial Modelling Environment and distributed throughout each leopard's 95% KDE home range with sample sizes matching that for each individual animal. The sum of generated random samples was equal to available points derived from leopard GPS fixes (total n= 7576) as a means to achieve a 1:1 ratio (Koper and Manseau, 2012).

3.2.6 Fourth Order Resource Selection Functions

For fourth resource selection functions, it was predicted that leopards would choose to hunt and kill prey in specific areas within their home range. For cluster identification, Home Range Tools (HRT) (Rodgers *et al.*, 2011) was used to identify the distances between consecutive leopard fixes in ArcGIS. While leopard collars were programmed to continuously record GPS fixes every 3 hours and twenty minutes, longer intervals would occasionally occur as a result of satellites being unable to communicate with the collar. Such acquisition failures were most likely due to the animals being located in an inaccessible area (such as rocky shelter, dense vegetation) (Swanepoel, Dalerum and van Hoven, 2010). Microsoft Excel 2013 (Microsoft Corp., Redmond, WA, USA) was used to determine the time intervals between all consecutive fixes for each individual animal. Following this, conditional statements were used to identify

potential clusters for every individual animal based on three or more consecutive fixes ≤ 50 metres apart (Pitman, Swanepoel and Ramsay, 2012) within a period of ten hours or more. As leopards will often leave their kills only to return to resume feeding (Bailey, 1993), clusters appearing ±24 hours within 50 metres of the previous cluster were classified as one event. The centre for each potential cluster (n=170) was given an ID, separated, and compiled into a separate CSV file.

To confirm the location of kills (ground truthing), 50 metre buffers were created at the centre fix of each individual cluster as a means to control for where extensive search efforts should take place (Blecha and Alldredge, 2015). All qualified clusters and their corresponding buffers were imported into a GPS device (Garmin 62S GPS) for survey. Search efforts began at the centre of the cluster and dispersed out until either the edge of the buffer was reached, or the kill was found. Clusters were given a binary indicator signifying either the presence (1) or absence (0) of a prey item. Given the rugged terrain, age of some clusters, and the inability to access certain properties, it was impossible to ground truth every potential kill.

Unlike second and third order RSFs, where an equal number of points were generated randomly throughout the scale of interest (use/available design) (Manly *et al.*, 2002), this analysis of 465 metre circular buffers surrounding each kill (the average distance between each fix) followed by generating 20 available fixes from within each buffer (Boyce *et al.*, 2003; Northrup, Stenhouse and Boyce, 2012). This intensive spatial and sampling protocol was utilised to control for the small sample size of kills (n=170) as well as to allow for a fine-grained multiscale analysis where kill sites can be assumed to be independent from other behaviours that would occur at courser scales. Thus, if leopard kill sites are dependent on specific environmental variables then the percentage of these attributes should be dissimilar compared to what is found within an entire study area.

3.2.7 Data Compilation, Analysis, and Validation

75% of available data (training data) was used for RSFs (Johnson *et al.*, 2006). Candidate RSFs were produced through generalized linear mixed-effects

models (GLMM) with a binomial error structure and logit link function (lme4, 2015) in R Studio. In this case, binomial response variables included 1 which represents used leopard locations whereas 0 represents available (random) locations (Rostro-Garcia *et al.,* 2015). Leopard ID and sex were used as a random intercepts for every scale of analysis (second, third, and fourth RSF) to control variability in sample sizes due to either collar malfunction or individual mortality as well as the lack of spatial independence found between leopard home ranges (Gillies *et al.*, 2006). The remaining 25% of the data (test) was used to confirm the final resource selection function through cross-validation (Johnson *et al.*, 2006).

The high correlation found between categorical habitat types and NDVI promoted the inclusion of only one (NDVI). AIC values from top candidate models suggested that NDVI models performed overall better compared to candidate models (Appendix 2, Tables S2.1 and S2.2 and S2.3) including categorical habitat types. All possible model combinations were generated through the MuMin package (Barton, 2015) in R studio (Version 0.98.1103). Akaike Information Criteria (AIC) was used to select the most parsimonious candidate model with the lowest score.

The top RSF model was projected in ArcGIS and the raster calculator (Spatial Analyst) was used to calculate and spatially project the probability of use for each 30 x 30 raster cell. To do this, coefficients from the top log linear model (β_1) were multiplied by the corresponding raster or vector layers representative of predictor variables (x_p) (Baigas *et al.*, 2010) through the following equation:

$$w(x) = \exp(\beta_0 + \beta_1 x_1 + \cdots + \beta_p x_p)$$

Linear stretching was applied to the resulting raster projection to improve visual interpretation (Johnson, Seip and Boyce, 2004). In doing so, the smallest (w_{min}) and largest (w_{max}) RSF values were scaled to values between 0 and 1 (Johnson, Seip and Boyce, 2004) through the following formula:

$$\widehat{w} = \left(\frac{w(x) - w_{min}}{w_{max} - w_{min}}\right)$$

Where, w^{min} and w^{max} signify the smallest and largest RSF values (Johnson, Seip and Boyce, 2004; Baigas *et al.*, 2010). The 25% leopard test data was then overlaid onto the rescaled RSF layer, and the values extracted ($\widehat{w}$) were separated into ten probability bins (0-0.1, 0.1-0.2, etc.) (Johnson, Seip and Boyce, 2004). Spearman's Rank Correlation was used to compare the frequency of points within each bin (Boyce *et al.*, 2002) with a strong positive correlation indicating a reliable RSF predictive model with the majority of test data approaching the scaled value of 1 (Johnson, Seip and Boyce, 2004).

3.3 Results

3.3.1 Second Order Resource Selection Functions

The best model contained significant, positive relationships for elevation, slope, ruggedness, and NDVI variables (Table 3.1; but see Appendix 2 Figure S2.4 for top alternative categorical habitat model). Collectively, these variables highlight selection for the mountain range itself in comparison to the relatively flat, low-lying, and agricultural areas featured off the mountains. There was a significant, negative relationship concerning leopard home range selection and urban areas, suggesting leopards actively avoid human settlements when establishing home ranges within the landscape. Leopards were more likely to establish home ranges in areas with Northern, Western and Southwestern facing aspects compared to others, although all estimates were positive in comparison to the reference category (flat ground) suggesting further selection for mountainous topography. The best model was a significant improvement over the null model where habitat selection was in proportion to availability (chi squared test: p = <0.0001). Projection of the model revealed large areas of suitable habitat within the Soutpansberg (Figure 3.1) and model validation suggested very good predictive performance for estimating second order leopard RSF's (r_s=0.898, n = 10, p=0.0004).

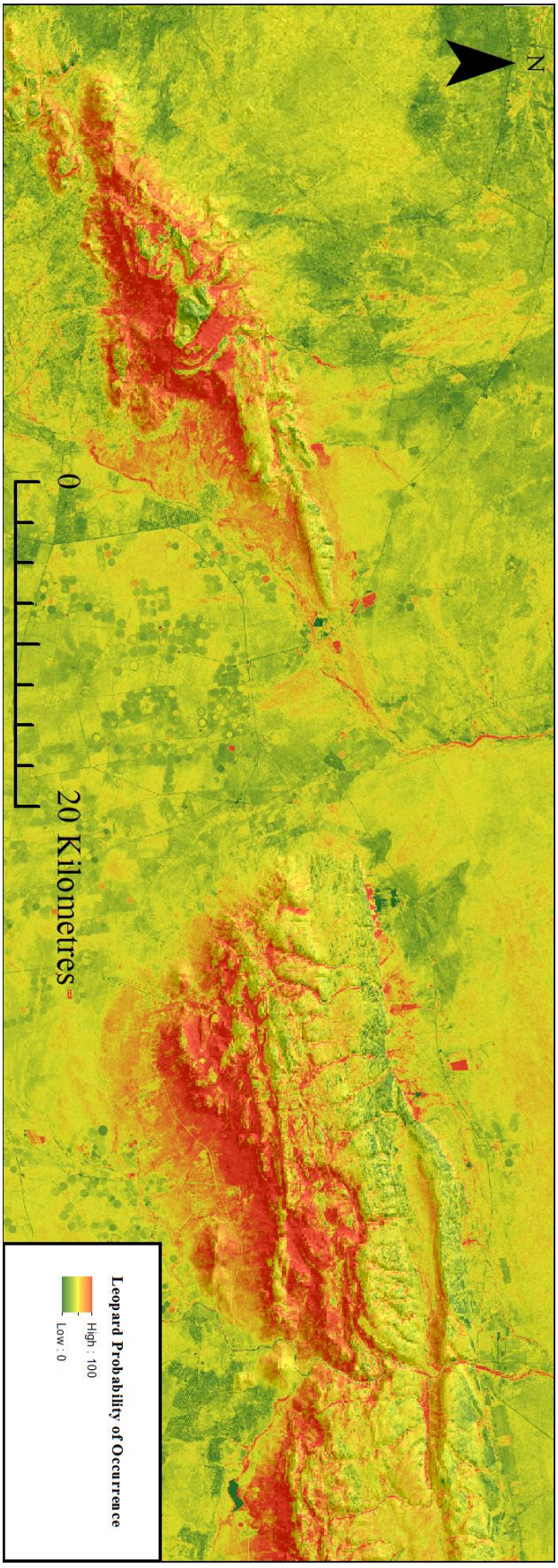

Figure 3.1 Second order resource selection (home range selection) for leopards in western Soutpansberg Mountains.

Table 3.1 Coefficients for the top binomial GLMM model for leopard home range selection (2nd Order) with use/available (leopard presence/absence) as the dependent variable. Bold P values represents a significant relationship.

Fixed Effects	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-6.55E+00	6.34E-01	-10.33	**<0.001**
Aspect (E)	3.45E-01	5.69E-01	0.61	0.545023
Aspect (N)	1.00E+00	5.68E-01	1.76	0.078649
Aspect (NE)	6.28E-01	5.70E-01	1.1	0.270149
Aspect (NW)	7.33E-01	5.69E-01	1.29	0.197608
Aspect (S)	7.71E-01	5.67E-01	1.36	0.173887
Aspect (SE)	4.28E-01	5.68E-01	0.75	0.450666
Aspect (SW)	9.81E-01	5.68E-01	1.73	0.084397
Aspect (W)	9.58E-01	5.70E-01	1.68	0.093026
Elevation	8.37E-04	1.18E-04	7.11	**<0.001**
NDVI	7.01E+00	1.92E-01	36.48	**<0.001**
Ruggedness	1.60E+01	4.34E+00	3.68	**0.000232**
Slope	8.78E-03	2.72E-03	3.23	**0.001244**
Distance from Human Settlements	6.03E-05	8.43E-06	7.15	**<0.001**

3.3.2 Third Order Resource Selection Functions

7576 leopard GPS fixes were utilised for Third Order RSFs. Mean 95% home range sizes equated to 29.4 ± 10.3 km^2 (range: 14.9-50.2 km^2, n=8) with males having larger home ranges than females (males: $\bar{x}$=33.03 ± 9.02 km^2, n=6; females: $\bar{x}$=18.6 ± 5.28 km^2, n=3.2).

The top candidate model (Table 3.2) for third order selection included NDVI, elevation, aspect, and distance from urban areas. Areas with higher NDVI values, an index of vegetation cover, were significantly chosen more by leopards compared to less vegetated areas within their home ranges. Replacement of NDVI with a categorical habitat variable suggests a strong preference for northern mistbelt forest (Appendix 2, Table S2.5). This is despite the fact this habitat only accounts for 9.92% of the area found within their merged home ranges. Urban areas were again significantly avoided for home range utilisation with leopards having tendency to utilise elevated areas within their home range.

Additionally, a Chi-Squared test between the top 3rd order RSF model was a significant improvement over and the null model rejected the hypothesis that the probability of occurrence for leopards was uniform throughout their home range (p = <0.0001) Projection of the model (Figure 3.2) and validation against the control data indicated that the top candidate model had a very strong predictive performance (r_s=0.898, n = 10, p=0.0004).

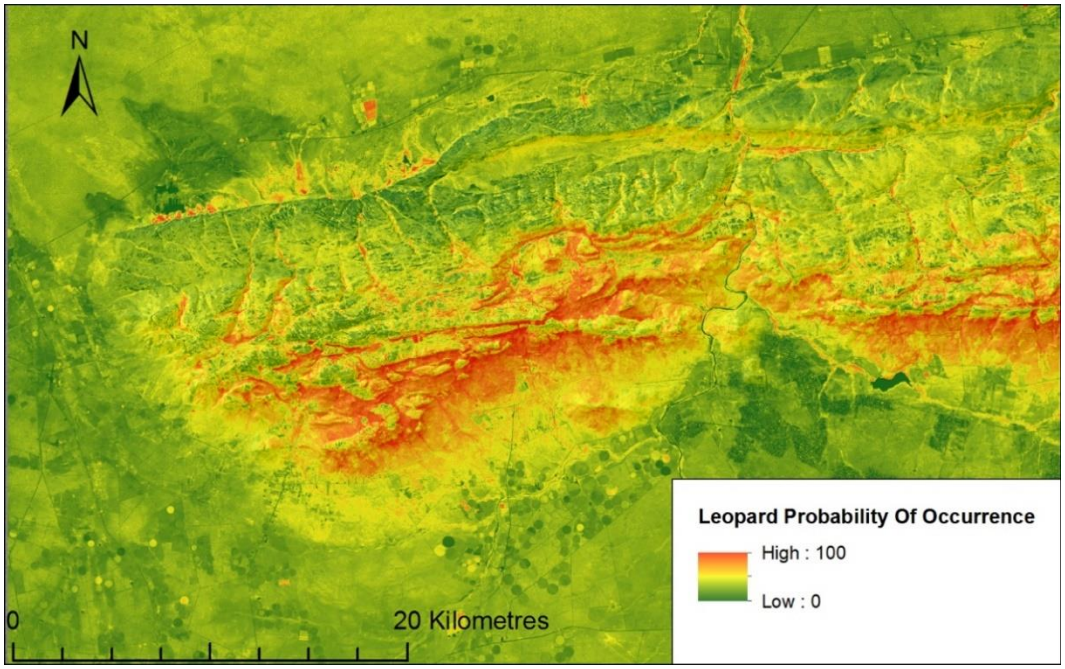

Figure 3.2 Third order resource selection (utilisation of home ranges) for leopards in western Soutpansberg Mountains.

Table 3.2 Coefficients for top binomial GLMM model regarding leopard selection within home ranges (3rd Order) with use/available (leopard presence/absence) as the dependent variable. Bold P values represents a significant relationship.

Fixed Effects	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.28E+00	7.97E-01	-2.856	**0.00429**
Aspect (E)	-2.79E-01	7.71E-01	-0.362	0.71772
Aspect (N)	4.80E-02	7.70E-01	0.062	0.95024
Aspect (NE)	-6.23E-02	7.71E-01	-0.081	0.93557
Aspect (NW)	1.62E-01	7.71E-01	0.21	0.83338
Aspect (S)	-2.81E-02	7.69E-01	-0.037	0.97082
Aspect (SE)	-2.59E-01	7.69E-01	-0.336	0.73661
Aspect (SW)	1.17E-01	7.70E-01	0.152	0.87898
Aspect (W)	3.36E-01	7.71E-01	0.436	0.66315
Elevation	1.97E-04	1.21E-04	1.636	0.10191
NDVI	2.95E+00	1.89E-01	15.647	**<0.001**
Distance from Human Settlements	2.82E-05	9.51E-06	2.968	**0.003**

3.3.3 Fourth Order Resource Selection Function

For fourth order resource selection functions, leopard kills (170) were assessed against 2580 randomly generated (available) points. The top model (Table 3.3 but see Appendix 2 Table S2.6 for top alternative categorical habitat model) contained just a single parameter, NDVI. While non-significant, leopard kill site selection was in areas of high NDVI and thus vegetation cover. Validation confirmed the strong predictive ability for the control data (r_s=.887, n = 10, p = 0.0006) and the top model for 4th order analysis was significant against the null model of leopards hunting and killing prey items uniformly throughout their home range (p = 0.0469) (Figure 3.3).

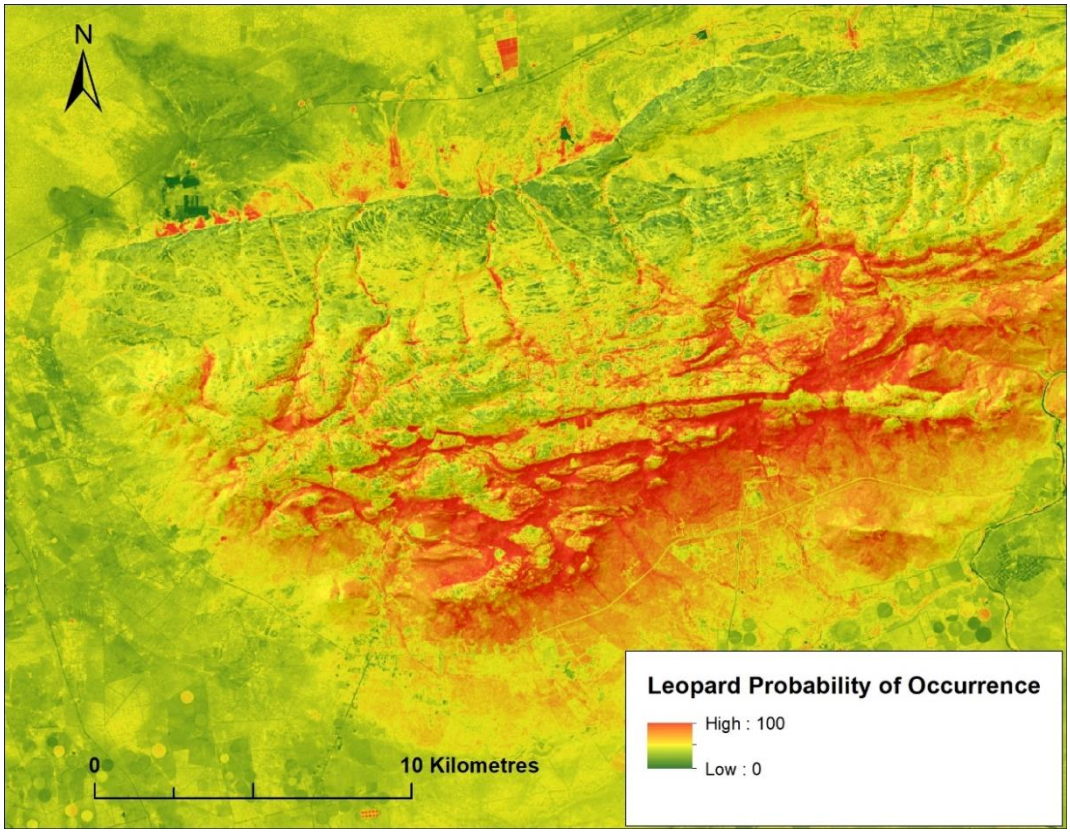

Figure 3.3 Fourth order resource selection (utilisation of home ranges) for leopards in western Soutpansberg Mountains.

Table 3.3 Coefficients for top binomial GLMM model regarding leopard kill site selection (4th order) with use/available (leopard kill presence/absence) as the dependent variable. Bold P values represents a significant relationship.

Fixed Effects	Estimate	Standard Error	Z Value	P Value
Intercept	-3.9126	0.4871	-8.033	**<0.001**
NDVI	1.4654	0.7530	1.946	0.0516

3.4 Discussion

There is a hierarchal scale of range selection for leopards residing in western Soutpansberg that is likely linked to the availability of environmental characteristics that promote fitness within the confines of the mountains as well as the avoidance of human dominated landscapes. My results suggest that for home range selection, leopards select for environmental variables that are positively associated with the mountain range such as high NDVI values, ruggedness, elevation and slope. Leopards also avoid low lying areas where

human settlements are abundant. From within their home range, leopards will select for forested or densely vegetated areas compared to more open habitats. This is may be due to the abundance of preferred prey items, ambush cover, and uniform distribution of water that is characteristic of the densely vegetated areas within their home range. Leopards also avoid human settlements on the periphery of their home range. The results from the 4th order RSF provide insight that leopards may not have a specific preference for environmental variables when deciding to hunt and consume their prey yet may do so homogeneously throughout their home range.

The eight collared leopards had variable home range sizes with males having larger home ranges than females. The largest home range (50.2 km^2) was a male that lived in the northern part of the mountain range whereas a female living in the most southern portion of the mountain had the smallest home range (14.2. km^2). Mean home range sizes for all males (N=6) living in the southern part of the mountain range was 29.5 ± km^2. In addition, mean home range sizes for females (N=2) was 23.25 ± km^2. Previous research had suggested that leopard population densities in the northern portion of the western Soutpansberg may be lower due to the aridity of the environment which, in turn promotes a lower abundance of prey (Chase Grey 2011). The results from this analysis indeed suggest that leopards are more likely to establish home ranges on the southern side of the mountain. It seems possible that the greater presence of forests, and overall, moister environment that is characteristic of the southern side of western Soutpansberg have an impact on the abundance of prey, and as a result, promote higher leopard densities.

Leopards in western Soutpansberg clearly selected specific environmental attributes within the mountain range, including areas featuring high elevation, slope, ruggedness, and high NDVI values while choosing home ranges. These results complement previous research which suggests that surface ruggedness and NDVI correlate to leopard habitat suitability by providing abundant prey, and beneficial vegetation for cover (Swanepoel *et al.*, 2013).

Leopards significantly avoided human settlements while simultaneously selecting for areas exhibiting higher elevations for both second and third order

resource selection functions. Leopards have been found to select for refuge areas such as mountainous areas when pressured by competition from superior predators or humans (Sunquist and Sunquist, 2002; Constant, Bell and Hill, 2015). Given that leopards in Soutpansberg are frequently persecuted by humans through legal or illegal hunting (Chase Grey *et al.,* 2013), it seems that leopards will likely avoid human settlements in favour of areas where competition with humans is lowered. The presence of unsuitable and heavily fragmented habitats, as well as a lack of primary prey within human dominated landscapes, may also drive leopards to avoid heavily populated areas while simultaneously selecting for more intact and prey rich environments such are those that are found within the mountains (Swanepoel *et al.*, 2013).

Although leopards avoid human settlements, distance from cultivated areas was not included in the top models for second, third, and fourth order resource selection functions. While it is possible that leopards may avoid such areas to a slight degree, only a small number of cultivated areas overlapped with the leopard home ranges in the mountains and were surrounded by preferable habitat or were located on the periphery of the mountains and thus, on the very edge of home ranges for leopards. Despite this, the final projections for both second and third RSFs show that agricultural areas located in low lying areas off of the mountains to be characteristic of low habitat suitability. Leopards may possibly show avoidance when agricultural areas become more homogenous on the landscape as well as when human populations increase within the vicinity of such areas.

While previous research found that water was a driving factor behind leopard second order resource selection functions (Simcharoen *et al.*, 2008; Mondal, Sankar and Qureshi, 2013), the top candidate models in this analysis did not include it as a variable. The possible reason for this is the uniformity of water sources on the landscape, as well as the lack of migratory prey species that would be driven to water sources. Balme (*et al.,* 2007) also found that water was not a significant variable for leopards residing in the Phinda Private Game Reserve, which may have been due the constant availability of water sources and as a result, a lack of congregation of items near these features.

While previous studies have found that large felids select specific habitats to kill and consume prey at the fourth order (Davidson *et al.,* 2012; Rostro-Garcia *et al.,* 2015), the best model (over the null) suggests that no environmental variable used in this study was significant for determining where leopards consumed their prey. Similar findings have also been reported by Gese, Terletzky and Cavalcanti, (2016) who determined that habitat characteristics did not define the location of a kill.

Given their clear selectivity for areas with higher NDVI values (such as forests) for both second and third order resource selection, it is possible that leopards restrict where they hunt, kill, and consume their prey to densely vegetated areas. Additionally, if their primary prey and adequate hunting grounds are uniformly distributed throughout the preferred areas of their home range, then it is possible that leopards will utilise all available areas to hunt. The vast majority of primary prey have a preference for canopied or densely vegetated areas such as forests and woodlands. Bushbuck residing in western Soutpansberg have a preference for areas with abundant tree canopy cover while avoiding both rocky and open grassland areas that are devoid of trees (Brock, Nortje and Gaigher, 2003). Equally, common duikers have been shown to avoid rocky and bare areas in favour of more densely vegetated areas such as tall grasses and "wooded islands" (Abu Baker and Brown, 2014).

As visual hunters, it has been suggested that leopards may be constrained to stalk prey in areas with intermediate vegetation coverage (Balme, Hunter and Slotow, 2007). However, several studies have shown that forest dwelling leopards may overcome hunting in denser environments by adapting other hunting strategies such as waiting for prey items to come close followed by a quick ambush (Hart, Katembo and Punga, 1996; Jenny and Zuberbühler, 2005).Given that the northern side of the western Soutpansberg is more arid and likely provides a patchier distribution of prey as well as adequate hunting areas, leopards residing there travel greater distances in order to locate suitable hunting grounds which, in turn, may lead to a larger home range.

While this analysis utilised a more conservative method for cluster identification compared to previous studies that would often use two or more

consecutive fixes at greater distances (i.e. 100 or 200 metres apart) (Anderson and Lindzey, 2003; Tambling *et al.*, 2010), the cluster classification chosen for this study was favoured for several reasons. The time interval between fixes (3 hours and twenty minutes) creates a level of ambiguity when identifying clusters consisting of only two fixes. Additionally, in some cases, ground truthing may be futile due to the amount of time that had passed as it is probable that the remains of older prey carcasses would be transported by scavengers (such as brown hyaenas; *Hyaena brunnea*), water, or wind, or concealed due to vegetation growth. While utilising three clusters (rather than two) may bias this analysis for where leopards choose to hunt, kill, and consume medium to large sized prey rather than prey of all sizes, the importance of species such as bushbuck and common duiker in leopard diet as confirmed through both ground truthing and scat analysis (Schwarz and Fischer, 2006; Chase Grey, 2011; Chase Grey, Bell and Hill, 2017; Williams *et al.*, 2018) is highly suggestive that these methods were appropriate for fourth order resource selection in this study.

The results from the 2nd order resource selection functions suggest that there is little to no connectivity between leopard populations in the western Soutpansberg and the Blouberg Mountain Reserve despite both areas displaying suitable habitats while simultaneously being within close proximity of one another. This is likely due to the lack of corridors of suitable habitat that would allow leopards to safely move between both ranges. Previous research suggests that mortality due to human persecution seems to be greater in low lying areas surrounding both mountain ranges (Chase Grey, 2011; Constant, Bell and Hill, 2015). This is most evident on game farms found in low lying areas where suitable habitat for leopards exist, yet, where mortality is high due to human persecution (Chase Grey, Kent and Hill, 2013; Constant, Bell and Hill, 2015). In this case, the western Soutpansberg may act as a population source for leopards where dispersing individuals are likely to succumb to mortality in prey-rich, but dangerous areas such as game farms and communal farms outside of the mountains.

Given the anthropogenic pressures found in areas that are otherwise suitable habitats, it seems probable that both the western Soutpansberg and Blouberg mountains act as refuges where natural prey are still abundant and yet where competition with humans is low. Thus, the results from this analysis should only be interpreted as leopard habitat suitability in a human altered landscape that does not reflect potentially suitable habitats if anthropogenic pressures were depressed.

By identifying suitable leopard habitat, the results from this analysis have the potential to aid in recovery efforts for a declining population (Williams *et al.*, 2017) living on the periphery of a heavily human modified landscape and may be beneficial in developing conservation priorities regarding land use management and the protection of key habitats that are advantageous towards leopard population sustainability. As apex predators have the potential to facilitate ecological stability through trophic interactions (Estes *et al.*, 2011), the identification, prioritisation, and overall, protection of viable leopard habitats may also be greatly beneficial towards sustaining the biodiversity in the already ecologically altered ecosystem (Hahn, 2006).

Given that the focal animals in this analysis were confined to the Western most portion of the Soutpansberg Mountains, it is highly recommended that future researchers focus their efforts on the occupancy, density, and behavioural ecology of leopard populations located in the central and eastern portions of the mountain range. This would allow for the identification and conservation of refugia throughout other parts of the mountain range, which can promote immigration and population recovery (Pitman *et al.*, 2015). In addition, by doing so would also allow for a greater understanding of the connectivity found between subpopulations throughout the Soutpansberg Mountains while simultaneously providing insight on whether the western Soutpansberg acts as attractive sink.

Chapter 4: Spatial and Temporal Variability in Activity levels in Leopards Residing in an Afromontane Environment

Abstract

Animals must expend energy to conduct vital behaviours such as searching for food and reproduction. In doing so animals must choose where and when to be active in order to enhance foraging opportunities while simultaneously avoiding the risks imposed by potential threats. An over expenditure of energy has been shown to reduce fitness levels that can lead to a decline in populations for certain species. With the aid of dual axis accelerometers, I explored whether abiotic and biotic factors led to spatial and temporal variation in activity patterns for leopards residing in the western Soutpansberg Mountains, South Africa. My results showed that leopards are predominantly crepuscular throughout the year, but also shift their activity levels in response to weather conditions such as rain, wind speed, and temperature. I also found that leopards spatially reduced their activity in topographically complex and highly vegetated areas. Finally, leopards temporally shifted their activity patterns while in anthropogenic habitats by reducing diurnal activity suggesting that such areas may be perceived as potentially dangerous.

4.1 Introduction

Animals expend energy during processes such as food acquisition, reproduction and sociality (Bailey, Udoh and Young, 2014; Humphries and McCann, 2014). Optimal foraging theory suggests that animals should minimize their total energy spent in response to total energy acquired as a means to maximise fitness levels and survival (Stephens, Brown and Ydenberg, 2007). As a response to such trade-offs, animals adopt activity schedules that allow for the maximisation of energy intake throughout time, while simultaneously avoiding predation (Schoener, 1974; Kronfeld-Schor and Dayan, 2003). Animals respond to a range of biotic and abiotic factors (Scharf *et al.*, 2016) and a greater understanding of such processes has the potential to yield insight into not only

how species interact with their environment, but also how animals may respond to anthropogenic landscapes.

Animal activity patterns are most often described throughout the 24-hour cycle as a response to light intensity (Bennie *et al.*, 2014). Most animals are considered to be active either during the day (diurnal), night (nocturnal), at dusk and dawn (crepuscular), and rarely, throughout the 24 hour cycle (cathemeral) (Bennie *et al.*, 2014). Such schedules are primarily reinforced through behavioural, environmental, and physiological adaptations that constrain or enhance when a species is most active (Kronfeld-Schor and Dayan, 2003). Despite this, many species exhibit some levels of fluidity in their activity budgets and may shift the times at which they are most active in response to conditions that potentially impact fitness (Kronfeld-Schor and Dayan, 2003). Such conditions include predator avoidance (Lima and Dill, 1990), foraging efficiency (Pavey *et al.*, 2001) and competition avoidance (Johnston and Zucker, 1983). For example, Valeix and colleagues (2007) found that several species of ungulates in Hwange National Park, Zimbabwe temporarily shifted their activity patterns in the dry season as a means to avoid interactions with elephants (*Loxodont africana*) at waterholes. In an experimental study, bank voles (*Clethrionomys glareolus*) in an enclosure that were previously more active at dawn, switched their activity levels to both day and night in order to avoid the presence of an introduced (and crepuscular) weasel species (*Mustela nivalis*) (Jędrzejewska and Jędrzejewski, 1990).

A complex interaction between physiology and behaviour often influences when animals are active (Kronfeld-Schor and Dayan, 2003), combined with extrinsic factors ranging from predator (including human) avoidance (Nelson and Vance, 1979; Ditchkoff, Saalfeld and Gibson, 2006), weather (Erickson and West, 2002) and the natural diel cycles in light intensity (Daan, 1981). Furthermore, movement may spatially fluctuate across the landscape (Shepard *et al.*, 2013). This is especially true in terrestrial animals that reside in areas which exhibit variable levels of environmental heterogeneity that may differ in topography (Wall, Douglas-Hamilton and Vollrath, 2006; Martins and Harris, 2013) , vegetation cover (Mosser *et al.* 2014), and even substrate thickness

((Wilson, 1991). Movement in itself is inherently costly (Delong, Hanley and Vasseur, 2014; Humphries and Mccann, 2014) and animals must invest in areas that provide the greatest energetic gain (through foraging), and are less metabolically costly to travel through (Shepard *et al.*, 2013) while simultaneously avoiding predation (Lima and Dill, 1990).

Large carnivores not only have some of the largest home ranges for their body size (Carbone, Teacher and Rowcliffe, 2007), they must also traverse through widespread areas in pursuit of prey, something which has the potential to be considerably more costly than the attack itself (Laundré, 2014). As such, the energetic costs of movement for some large carnivores (e.g. *Panthera leo, Ursus maritumus*) were recorded to be two or three times greater compared to other mammals of similar size (Carbone, Teacher and Rowcliffe, 2007). As carnivores may constantly sustain maximum energy outputs , they may be highly susceptible to even the slightest alteration in habit quality or prey abundance (Gorman *et al.*, 1998) which has contributed to their vulnerability to extinction throughout the world (Ripple *et al.*, 2014).

To limit the amount of energy spent in the pursuit of prey, carnivores hunt in areas where prey are either more abundant (Murray, Boutin and O'Donoghue, 1994) or where the probability of catching them is greater (Grant *et al.*, 2005; Balme, Hunter and Slotow, 2007). In addition, carnivore movement patterns may be influenced by avoiding dominant carnivore species and areas of perceived risk (Vanak *et al.*, 2013), as well as ease of transport, (Dickson, Jenness and Beier, 2005), and reproduction (i.e. searching for potential mates, communicating and denning) (Wilmers *et al.*, 2013). For example, wolves (*Canis lupis*) in Alberta and Saskatchewan (Canada) increased their movement on manmade linear features (i.e. roads, railroads) compared to forests, which most likely aided in the pursuit of prey or territorial monitoring (Dickie *et al.*, 2017). As such, the activity patterns found in carnivores can be considered a dynamic process that is heterogeneous throughout the landscape in which they reside.

Large carnivores are primarily active during time periods in which the probability of successfully subduing and capturing prey increases. The time period in which they hunt is often influenced by a combination of factors

ranging from prey activity levels (Monterroso, Alves and Ferreras, 2013) to when specific abiotic conditions may be beneficial (or disadvantageous) towards specific hunting techniques (Cozzi, Broekhuis, Mcnutt, *et al.*, 2012). For example, while many cursorial predators such as wolves (Theuerkauf *et al.*, 2003), cheetahs (*Acinonyx jubatus*) (Broekhuis *et al.*, 2014), and African wild dogs (*Lycaon pictus*) will often take advantage of increased moonlight to aid in capturing their prey (Rasmussen and MacDonald, 2012), such conditions may be suboptimal for stalking predators such as lions (Packer *et al.*, 2011) and leopards (*Panthera pardus*) (Martins and Harris, 2013) who primarily rely on stealth and the cover of darkness.

Having the ability to live in an array of different habitats ranging from deserts, rainforests, grasslands, and even around urban areas, leopards are one of the most geographically widespread felid species (Jacobson *et al.*, 2016). This biogeographical characteristic may partially be explained due to their stealthy and solitary nature, incredibly catholic diet, and overall behavioural plasticity (Jacobson *et al.*, 2016).

As ambush predators, leopards rely on sufficient hunting coverage to successfully stalk and subdue prey (Bailey, 1993). As a result, leopards often prefer to hunt in areas exhibiting high or intermediate vegetation where the probability of catching prey is greater (Balme, Hunter and Slotow, 2007). In addition, leopards may prefer to be active in areas where dominant competitors (such as larger carnivores) are relatively absent. For example, Odden (*et al.,* 2010) found that leopards in Bardia National Park, Nepal were displaced to human dominated areas as a means to avoid competition with tigers (*Panthera tigris*). Pitman and colleagues (2013) found that leopards residing in a mixed-montane environment restricted essential activities (such as resting and hunting) to more elevated, rugged areas to avoid lions. Notwithstanding being displaced, topographically complex areas may prove to be advantageous for stalking predators by providing ample coverage for hunting (Bryce, Wilmers and Williams, 2017). Despite this, there has yet to be a formal assessment of how such areas impact activity levels in large felids in the absence of dominant carnivore species.

Unlike lions and cheetahs, who are primarily active either during the day or at night, previous research has found leopard activity patterns to be relatively fluid, changing as a response to habitat, prey availability and human presence (Jenny and Zuberbühler, 2005; Ngoprasert, Lynam and Gale, 2007; Martins and Harris, 2013). For instance, leopards in savannahs have often been documented to be nocturnal and/or crepuscular (Bailey, 1993; Balme, Hunter and Slotow, 2007) whereas leopards in rainforest environments are active throughout the day (Jenny and Zuberbühler, 2005). There have been several conflicting suggestions of why leopards shift to being primarily diurnal despite being considered to be crepuscular and nocturnal throughout much of their geographical range. For instance, although Sunquist & Sunquist (2002) suggested that leopards residing in predator-free landscapes will often switch their activity patterns to become more diurnal, several studies have implied the opposite effect; that is, in the presence of superior carnivore species, leopards became diurnally active as a means to avoid intraguild competition (Azlan and Sharma, 2006; Pitman *et al.*, 2013). Despite this, Martins and Harris (2013) found that leopards residing in Cederberg Mountains (South Africa) were still primarily nocturnal, despite living in a predator free environment (but see Norton and Henley 1987 who found leopards in the Cederberg Mountains to be primarily diurnal).

With the aid of dual axis accelerometers and telemetry data deriving from GPS collars, the primary objectives of this analysis were to assess how leopards in the western Soutpansberg Mountains (South Africa) vary their activity patterns in response to both a heterogeneous landscape as well as fluctuating levels of abiotic and meteorological conditions. Following Valeix and colleagues (2012), I also explored whether "the landscape of fear" applied to leopards that ventured into relatively dangerous human-dominated landscapes and whether such individuals modified their activity levels as a means to avoid conflict.

Previous research deriving from camera trap data determined that leopards in the Soutpansberg had crepuscular and nocturnal activity patterns that decreased significantly throughout the day (Fitzgerald, 2015). Despite this, the use of accelerometers that continuously recorded activity data allowed me to

monitor individual activity patterns at a finer spatial and temporal scale that permitted assessment of not just activity schedules as a whole, but also how leopards responded to both seasonal and meteorological variables. Accelerometers have proven useful in monitoring animal activity patterns through time and space without causing disturbance that may alter behaviour as a result of the presence of an observer (Brown *et al.*, 2013). I hypothesised that activity patterns recorded by accelerometers would accurately reflect patterns previously recorded by camera traps, and therefore, leopards would exhibit crepuscular and nocturnal activity (H1). Furthermore, I hypothesised that leopard activity levels would seasonally fluctuate between the seasons (H2).

Weather conditions such as wind speed and rainfall have the potential to mask movement and noise, and therefore may be beneficial for stalking predators. However, there has been little assessment on how such conditions influence activity patterns in solitary felids. Bailey (1993) observed that leopards tend to move less in warmer temperatures and significantly more on nights exhibiting moderate rainfall (and though were not influenced by wind-speed). I hypothesised that leopard activity levels would decrease with warmer temperatures and increase with heavier rains and stronger winds (H3).

As large carnivores will often avoid conspecifics in order to avoid conflict with individuals that have the potential to disrupt reproductive success, or harm (Klinka and Reimchen, 2002), I hypothesised that female leopards in western Soutpansberg would exhibit more diurnal activity compared to males (H4).

Most felids (including leopards) depend on denser vegetation as a means to stalk and subdue prey (Sunquist and Sunquist, 1989) and may often select closed habitats. As such, I hypothesised that leopards would spatially alter their activity levels in response to variables (e.g. vegetation structure, elevation, slope, and ruggedness) that enhance sufficient hunting coverage, as well as prey availability (H5). A recent analysis found the leading cause of death for leopards in the western Soutpansberg was due to retaliatory killing by humans in the form of snaring, poisoning and shooting (Williams *et al.*, 2017). As felids may move more rapidly through areas that are either less dense or that may cause

discomfort (such as urban areas) (Dickson, Jenness and Beier, 2005), I hypothesised (H6) that leopards would change their activity levels when in proximity to anthropogenic features including agricultural areas and proximity to human settlements.

4.2 Methods

4.2.1 Study Site

I conducted the study in the western Soutpansberg Mountains (Limpopo Province, South Africa) (central coordinates: 23°06'45.14"S 29°11'37.10"E). Considered to be a 'biological hotspot', the Soutpansberg Mountains is home to approximately 76% of South Africa's non oceanic birds (Berger *et al.* 2003), 36% of the country's reptile species (Berger *et al.* 2003) and 59.9% of South Africa's mammalian species (Berger *et al.* 2003). The Soutpansberg Mountains are temperate and have two seasons including a rainy season lasting from December to February and a dry season that lasts from May to August. In addition, average precipitation throughout the mountain range is highly variable, with the arid northern side of the mountain receiving roughly 367 mm of rainfall and the southern side experiencing roughly 3000 mm annually (Hahn, 2002) (Section 2.2.)

4.2.2 Leopard Collaring Methods, GPS and Activity Data Collection

Between June 2012 and December 2014, eight leopards (six males and two females) were captured with foot snares and sedated with either Zoletil or a Zoletil/Medetomidine combination by a South African Registered Veterinarian before being fitted with Vectronic GPS-PLUS collars (VECTRONIC, Aerospace, Berlin, Germany). Collars were programmed to take GPS fixes every three hours and twenty minutes and were designed to fall off 455 days after the collars were fitted (Section 2.4.3). Incorporated into the GPS collars were dual-axis sensors that constantly recorded activity on two different axes (X and Y) (Berger, Dettki and Urbano, 2014). As there was a positive correlation between the X and Y axis data, only the X-axis data were utilised in analysis (following Heurich *et al.* 2014). Activity values derived from sensors ranged from 0 (no activity) to 255 (high activity). In this instance, activity is referred to any

movement that was recorded, regardless of the position and behavioural state of the animal (Scheibe *et al.*, 1998) (Section 2.4.5) All data were downloaded regularly through an Ultra High Frequency (UHF) terminal.

4.2.3 Meteorological and Temporal Predictor Variables

In order to assess activity levels throughout the 24-hour diel cycle (H1), activity data were split into three categorical variables: diurnal (between sunrise and sunset on a single day), crepuscular (data that fell between 1 hour before and after sunrise and sunset) and nocturnal (falling one hour after sunset and one hour before sunrise) (Gutiérrez-González and López-González, 2017). In addition, as I hypothesised that leopards in the western Soutpansberg are primarily crepuscular (H1), the time difference found between each accelerometer signature and the closest sunrise/sunset (from http://aa.usno. navy.mil/) was calculated and utilised as a predictor variable. Day length (originating from http://aa.usno. navy.mil/) and meteorological variables (from an on-site SAEON (South African Environmental Observation Network) weather station) were used to determine if leopards shifted their activity as a response to fluctuating and seasonal shifts in light availability (H2) as well as weather conditions (H3). Accelerometer data were then averaged into half hour intervals (N=43447) and then synchronized with available weather and temporal data (time of day, day length, etc.) for analysis.

4.2.4 Landscape Predictor Variables

Several rasters (NDVI (Normalized Difference Vegetation Indices), slope, elevation, surface ruggedness) and vectors (distance from human settlements, agricultural areas, and rivers) were created and exported to ArcGIS10.3.1. (Environmental Systems Research Institute, Inc., Redlands, CA, USA) to assess whether physical environmental variables influenced leopard activity levels (H5).

All buildings within the study area were digitised with the aid of high resolution satellite imagery using Google Maps. In addition, agricultural areas (from Landsat imagery at a 30 metre resolution) were derived from the South African National Land Cover Map (2014) provided by the SANBI website

(http://bgis.sanbi.org/DEA_Landcover/project.asp). Urban and agricultural areas were isolated and converted into vector format through ArcGIS.

Topographic and waterway data (slope, elevation, rivers, and ruggedness) were created from a 30 metre resolution digital elevation model (DEM) provided by the Shuttle Radar Topography Mission (SRTM) and downloaded from the United Stated Geological Survey (USGS) Earth Explorer website (http://earthexplorer.usgs.gov/). Waterway data were created with the utilisation of the Optimized Pit Removal Tool extension (Centre for Research in Water Sources, Austin, TX) in ArcGIS. In addition, a ruggedness raster layer was created through the Benthic Terrain Modeller toolbox for ArcGIS (Rinehart *et al.*, 2004). A slope raster layer was created through the Spatial Analyst toolbox in ArcGIS.

NDVI has been proven useful in assessing how vegetation structure can impact wildlife activity levels (Pettorelli *et al.*, 2011; Mosser *et al.*, 2014). It was used in this analysis to assess how leopard activity levels fluctuate across the relatively heterogeneous vegetation communities of the western Soutpansberg.

Six 30-day Landsat-8 Operational Land Imager (OLI) and Thermal Infrared Sensor images (30 metre resolution) from within the collaring period (July, October, November 2013 and April, June, and August 2014) were downloaded from the USGS Earth Explorer website in order to create an NDVI composite. The dates utilised were seasonally divided between winter (June-August) and summer (November-January). NDVI was calculated for each month using the following equation (Tucker *et al.*, 2005)

$$NDVI_n = \frac{IR_n - R_n}{IR_n + R_n}$$

In this instance, IR (infrared) represents the 5th band whereas R (red) represents the 4th band. Monthly NDVI images were compiled with the use of the Image Analysis function in ArcGIS.

To evaluate whether activity levels varied spatially across the landscape, accelerometer data (through the X axis) deriving from collars were synced with

available GPS points (Berger, Dettki and Urbano, 2014). As accelerometers continuously stored data in two minute intervals, all averaged activity data falling between ten minutes before and after a GPS fix (recorded every 3 hours and twenty minutes) were utilised in this analysis. A portion of GPS data could not be synced with activity data as the accelerometer for one leopard malfunctioned; as a result, only 6279 samples (out of 7679) were utilised in this analysis. All synced GPS/activity points were projected into ArcGIS, spatially joined with environmental predictor variables and extracted for analysis.

4.2.5 Statistical Analysis

Activity data were separated into two different datasets. The first model (Model A) consisted of average activity separated into half hour intervals (N=43447) that were used to assess when leopards are active throughout the diel cycle (H1), how they responded to both seasonality (H2) and to meteorological variables (H3) and whether activity schedules varied by sex (H4). I developed a model consisting of combined GPS/ averaged activity data (N=6279) in intervals of 3 hours and twenty minutes that was used to assess how activity levels spatially fluctuated as a response to specific landscape attributes (H5 and H6). A post-hoc analysis was used to determine if leopards that went off the mountain (and into human dominated landscapes) shifted their activity schedules compared to individuals on the mountain.

Wind speed, temperature, and rainfall were included in the temporal analysis (Model A, N=43447) to measure whether leopards residing in an Afromontane environment responded to specific meteorological conditions. Day length was included in order to evaluate whether leopards altered their activity patterns in response to seasonally changing light conditions. Two variables were used to address when leopards were active throughout the diel cycle: 1) time of day (categorical factor consisting of diurnal, crepuscular, and nocturnal) and 2) the difference found between each accelerometer time signature and the closest sunrise/sunset. In addition, sex of the individual was included as a predictor variable to assess if the activity schedules for males and females differed. Random effects for this model included individual ID (N=8), as well as the day number (N=835).

Elevation, slope, and surface ruggedness were included in the spatial model to assess if activity levels were influenced by heterogeneous topography. In addition, such variables were used to address if leopards responded to relatively low lying and flat areas off the mountains by shifting their behaviour. NDVI and distance from rivers were additional environmental variables included in Model B. Furthermore, distances from agricultural and urban areas were included in the model to assess if leopards reduced their activity levels when in proximity to human settlements. Given the variability in sample sizes between individuals, sex (N=2), and individual ID (N=8) were included as random effects.

Although the spatial analysis (Model B) was used to measure if leopards responded to human occupied areas both on and off the mountain, a more refined analysis was conducted to determine if the activity of leopards in more populated and heavily utilised (farming and ranching) areas differed from those that stayed in the mountains. To test whether leopards shifted their activity schedules to be more nocturnal as a means to avoid humans, all leopard data points were categorised as either being on the mountain (N=4216) or off of the mountain (N =2063) based on elevation and location. Mean elevation for leopards on the mountain was 1173.8 metres compared to 1049.5 metres for those off the mountain.

Included in this analysis were an interaction between the time of day (crepuscular, diurnal, and nocturnal) and whether the leopard was on or off the mountains, as well as the significant predictor variables from the full spatial model - NDVI and slope – but excluding distance from urban areas. Similar to the previous spatial model (Model A), random effects were sex and ID.

Three generalised linear mixed models (GLMM) with a gamma error structure and log link function (Bates *et al.*, 2015) were used to assess how activity levels varied spatially and temporally. Activity data were transformed by adding 1 to all values to fulfil the requirements for a gamma GLMM. All models were run in R studio (Version 0.98.1103; RStudio, Inc).

4.3 Results

Model A (temporal) assessed overall activity schedules (H1), how they differed by sex (H4), as well as how activity may fluctuate due to seasonal (H2) and meteorological (H3) conditions. A likelihood ratio test found the full model to be significant over the null model which only included random effects individual ID and day number (likelihood ratio test:$x^2 = 739.29, df = 7, p =< 0.0001$). As predicted (H1), leopards increased their activity at night and significantly decreased activity levels during daytime hours (Table 4.1). In addition, while day length had no significant effect on activity levels, leopards still responded to seasonally fluctuating changes in sunrise and sunset times by shifting activity to coincide with such periods. In addition, leopards were significantly more active during periods with heavy winds and rain but moved significantly less during warmer temperatures (H3). Lastly, male leopards were found to be more nocturnal compared to females who were more active during the day (H4) (Figure 4.1)

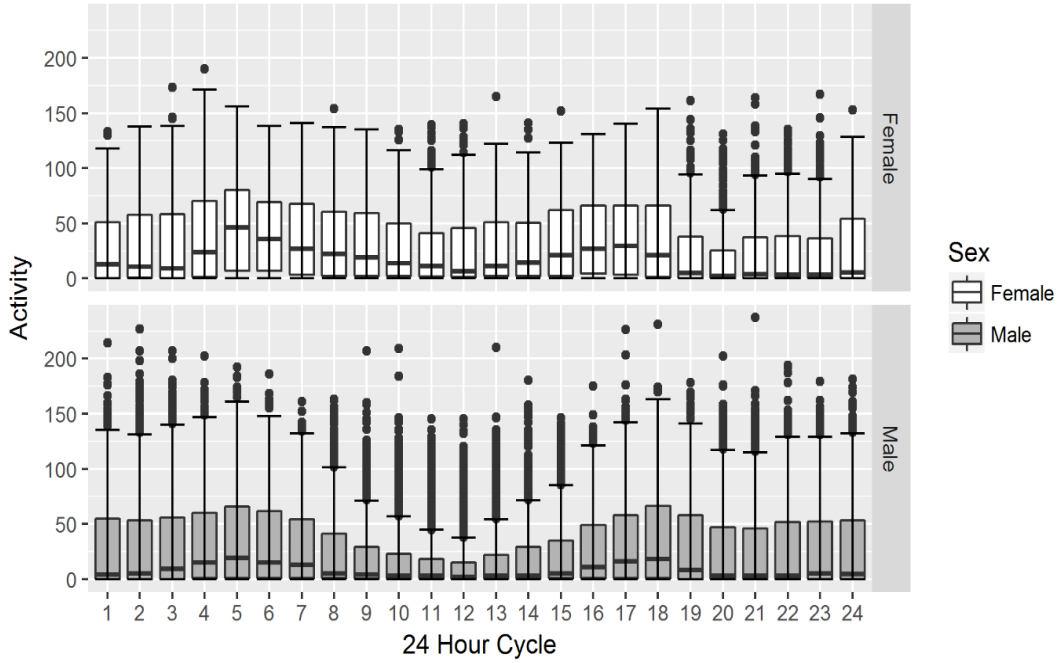

Figure 4.1 Boxplots (median, lower and upper quartiles, and one standard error) for female (white) and male (grey) leopard activity across the 24 hour cycle. Activity values range from 0 (low activity) to 255 (high activity).

Table 4.1 Coefficients for factors influencing leopard temporal activity from gamma error GLMM with leopard temporal leopard activity value as dependent variable. Bold P values represents a significant relationship.

Fixed Effects	Estimate	Std. Error	t Value	Pr(>|z|)
Intercept	3.643	0.232	15.698	**<0.001**
Wind speed	0.003	0.001	1.975	**0.048**
Rain	0.065	0.015	4.316	**<0.001**
Temperature	-0.020	0.002	-9.649	**<0.001**
Hours from Sunrise/Sunset	-1.931	0.103	-18.699	**<0.001**
Day Length	0.523	0.432	1.210	0.226
Sex (male)	-0.246	0.107	-2.300	**0.021**
Time Period (Nocturnal)	0.139	0.016	8.499	**<0.001**

The spatial model (Model B) included slope, surface ruggedness, elevation, distance from rivers, NDVI, as well as distance from agricultural and human settlements as predictor variables and assessed whether leopard activity levels vary spatially across the landscape (H5) (Table 4.2). The full model was a significant improvement over the null model which only included the random effects individual id and sex (likelihood ratio test: $x^2 = 102.5, df = 7, p =< 0.0001$). Of the topographic variables, leopards were significantly more likely to decrease activity on steeper slopes compared to relatively flatter areas, yet in contrast to my original predictions for hypothesis 5, elevation and surface ruggedness had no significant effect on leopard activity levels. Leopards were significantly less active in areas with denser vegetation. Distance from river systems and agricultural areas had no effect on activity. Leopards were significantly more active close to human settlements.

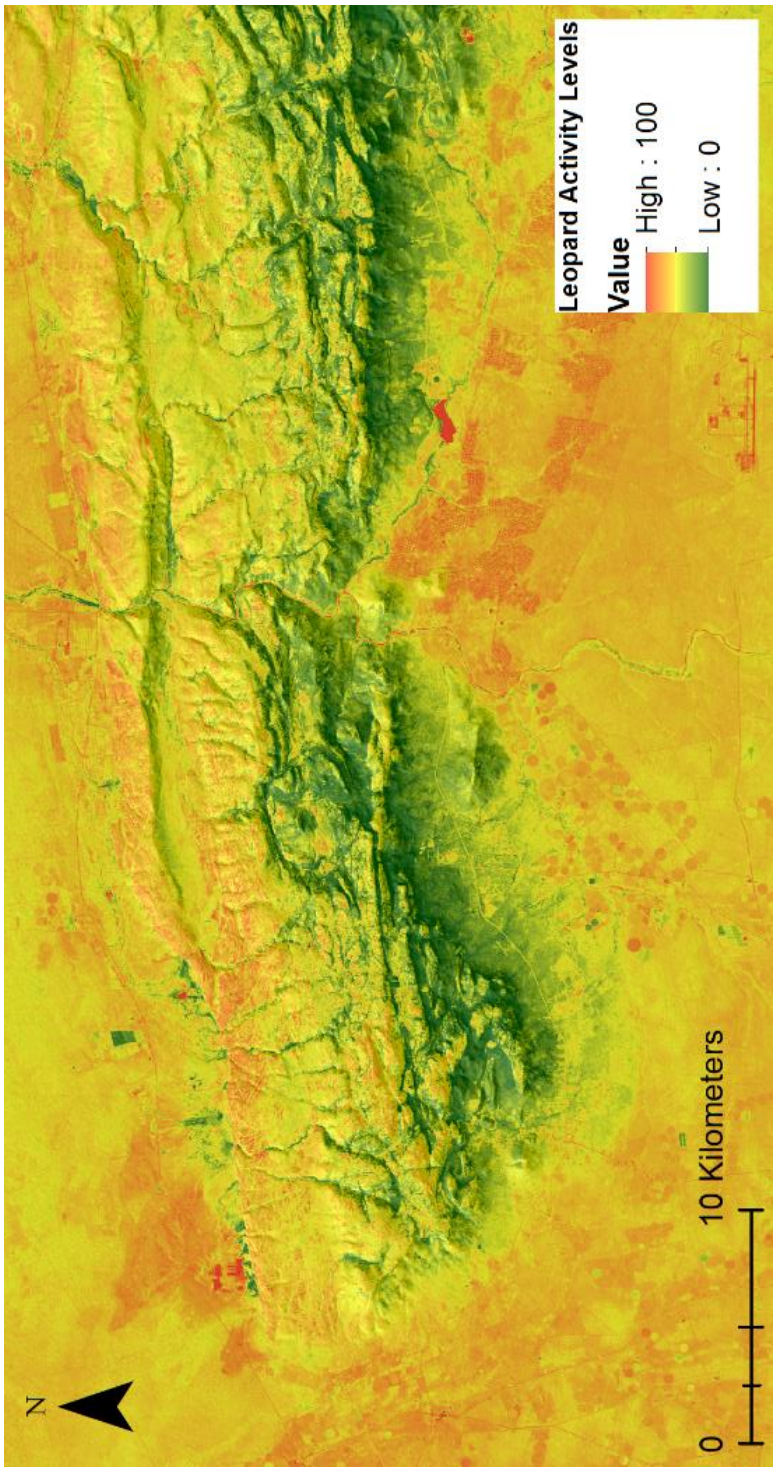

Figure 4.2 Projected leopard activity levels across the western Soutpansberg Mountains.

Table 4.2 Coefficients for trends in leopard spatial activity from gamma error GLMM (spatial activity values as dependent variable). Bold P values represents a significant relationship.

Fixed Effects	Estimate	Std. Error	t Value	Pr(>|z|)
Intercept	4.224	2.349	17.978	**<0.001**
Slope	-1.004	2.343	-4.286	**<0.001**
Surface Ruggedness	-7.334	3.831	-0.191	0.848
Distance from Agricultural Areas	-9.998	2.172	-0.460	0.645
Distance from Human Settlements	-1.245	3.548	-3.509	**<0.001**
Distance from River Systems	1.714	2.901	0.591	0.554
Elevation	5.764	1.210	0.476	0.633
NDVI	-1.171	1.766	-6.632	**<0.001**

As Model A showed that leopards in western Soutpansberg were primarily crepuscular and Model B demonstrated that focal leopards responded to human settlements by increasing activity levels, I assessed if leopard activity schedules shifted after they went off the mountains and into human dominated areas. Predictor variables included slope, an interaction between time of day and whether the animal was on or off the mountain as well as NDVI. A likelihood ratio test found the full model to be significant improvement over the null model which included slope, NDVI and the random effects individual ID and sex (likelihood ratio test:$x^2 = 128.95, df = 11, p =< 0.0001$). Leopards increased their crepuscular and nocturnal activity while off the mountain and close to human dominated areas such as towns, game farms, cattle ranches and agricultural areas (Table 4.3). In addition, an interaction between time of day and leopard presence (on/off the mountain) suggests that leopards that are physically off the mountain were more likely to increase their nocturnal and crepuscular activity levels compared to those on the mountain (and at a greater distance away from humans).

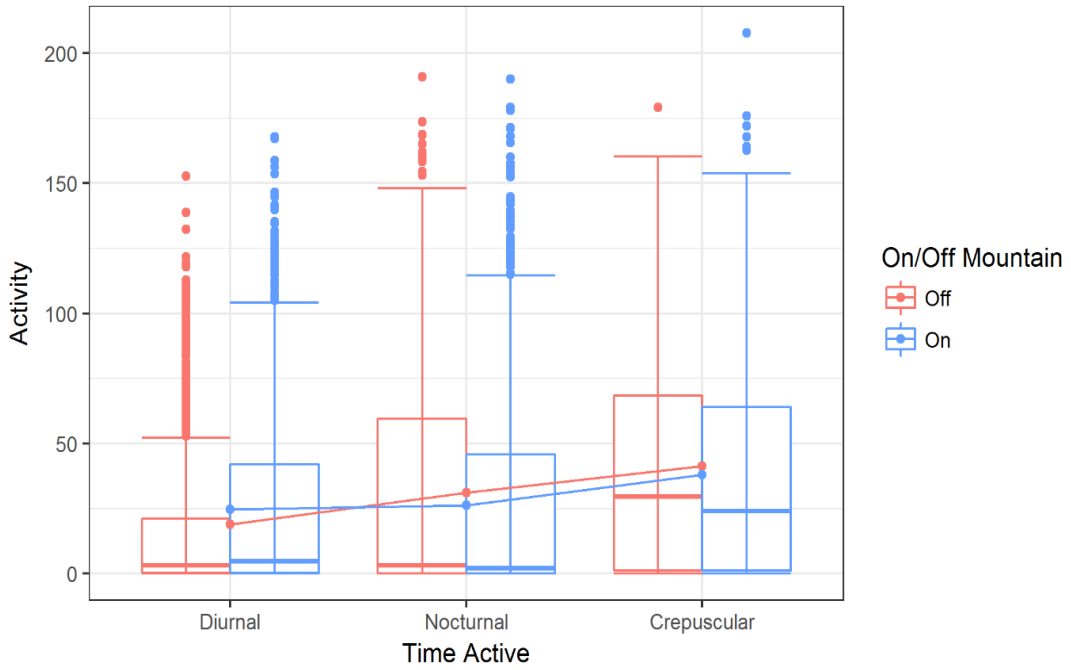

Figure 4.3 Boxplots comparing leopard activity both on (blue) and off (red) the mountain (mean (dotted lines) median (50% quantile), lower and upper quartiles, and standard error bars.

Table 4.3 Coefficients for trends in assessing leopard activity both on and off the mountain from gamma error GLMM (leopard activity values as dependent variable). Bold P values represents a significant relationship.

Fixed Effects	Estimate	Std. Error	T Value	Pr(>|z|)
Intercept	3.911	0.1690	23.143	**<0.001**
Slope	-0.010	0.0020	-5.159	**<0.001**
NDVI	-1.187	0.1744	-6.807	**<0.001**
On Mountain	0.2447	0.0623	3.929	**<0.001**
Time of Day: Nocturnal	0.3431	0.0676	5.072	**<0.001**
Time of Day: Crepuscular	0.7273	0.0873	8.322	**<0.001**
Interaction: Presence on Mountain/ Time of Day: Nocturnal	-0.3194	0.0813	-3.925	**<0.001**
Interaction: Presence on Mountain/ Time of Day: Crepuscular	-0.3235	0.1059	-3.053	**<0.001**

4.4 Discussion

Leopards in the western Soutpansberg show fluctuating levels of activity in response to environmental and anthropogenic conditions. Temporally, leopards in the western Soutpansberg are predominantly crepuscular and more active close to sunrise and sunset although males were more nocturnally active than females and transient males. In addition, the temporal model showed that leopards increased their activity levels during rainy and windy conditions and decreased activity when temperatures were higher. A spatial model found that leopards altered their activity levels throughout the landscape in response to vegetation structure (NDVI), slope, and distance from human settlements. Leopards ranging off the mountain and into anthropogenic habitats were more active at night compared to individuals that stayed on the mountains.

Temporally, leopards in the western Soutpansberg displayed primarily crepuscular activity and become more active around sunrise and sunset and at night and were least active around midday. These results complement data

collected from camera traps placed on the mountains which also suggest that leopard activity peak at crepuscular and nocturnal hours (Fitzgerald, 2015). Although leopards did not shift their activity schedules in response to day length, they altered their activity schedule in conjunction with seasonal shifts in sunrise and sunset times. Interestingly, these results contrast with the activity schedules found in leopards residing in the Cederberg Mountains (South Africa) that did not display fluctuating seasonal levels in activity (Martins and Harris, 2013). It seems likely that by seasonally shifting the time in which they are active to align with sunrise and sunset in the Soutpansberg, leopards may be able to continue to temporally overlap with the activity levels of their primary prey such bushbuck and common duiker (Fitzgerald, 2015) with the former prey species also exhibiting primarily crepuscular activity regardless of season (Wronski, Apio and Plath, 2006). These results complement the fluidity found in leopard activity patterns from other populations (Jenny and Zuberbühler, 2005; Bothma and Bothma, 2006).

Females were more active than males and while all leopards in this study were primarily crepuscular, there was variability between the sexes, with females being more diurnal than males (Figure 4.1). It is possible that females switched to diurnal activity in order to avoid conflict with larger males. Similar temporal avoidance has also been recorded in leopards in Bardia National Park, Nepal (Odden and Wegge, 2005) where females with relatively small home ranges and/or cubs switched their activity patterns to be more active throughout the day. Although neither collared female (N=2) was recorded with cubs during the study period; the small home ranges for females in the area (mean home range size = 18.9. km^2) coupled by substantial overlap with males most likely increased the chance of encounters between the sexes and therefore, promoted avoidance.

Leopards decreased their activity levels in response to warmer temperatures and responded to stronger winds and higher precipitation by increasing their activity. The negative relationship found between temperature and activity is most likely due to the fact they are less active during the hottest periods in the day (noon to late afternoon), something that has been reported for leopards

(Martins and Harris 2013) and other felid species including lions (Hayward and Hayward, 2007) and lynx (Heurich *et al.*, 2014).

One possible explanation for why leopards are more active during periods of heavier winds and higher precipitation may be due to the fact that both weather conditions have the potential to enhance hunting conditions. As sedentary ambush predators, leopards primarily rely on stealth and the element of surprise in order to successfully hunt. As such, times with moderate to heavy rainfall and stronger wind speeds may be advantageous by masking both auditory and olfactory senses in animals (Muñoz, Kapfer and Olfenbuttel, 2014; Cherry and Barton, 2017) and so decrease detectability. Such beneficial hunting conditions may be enhanced by the fact that leopards' primary prey (medium sizes ungulates) (Hayward, Henschel, O'Brien, Hofmeyr, Balme and G. I H Kerley, 2006) ruminate during such conditions to maintain homeostasis (Moquin *et al.*, 2010; Cherry and Barton, 2017) and therefore, may be less vigilant and more susceptible to predation (Cherry and Barton, 2017).

In support of hypothesis 5, the structure of the landscape influenced where leopards were most likely to be active or inactive. Leopards responded to thicker vegetation, heavily sloped areas, and greater distances from human features by reducing their activity levels (Figure 4.2). Leopards prefer to establish home ranges and utilise areas that are both topographically complex and densely forested (Chapter 3) and there are several possible explanations for why activity levels also decline in these habitats.

Previous scat analysis has shown that leopards prefer to hunt forest and thicket dwelling species such as common duiker(*Silvicapra grimmia*), bushbuck (*Tragelaphus scriptus*), vervet monkeys (*Chlorocebus pygerythrus*) and members of Hyracoidea (hyrax) (Stuart and Stuart, 1993; Schwarz and Fischer, 2006; Chase Grey, 2011). As forests only make up only 9.92% of the area found within the home ranges, leopards in my analysis most likely moved between forest patches in pursuit of prey.

Once in forest patches, however, they likely provide sufficient coverage to stalk and ambush potential prey while simultaneously minimising energy

expenditure. Previous research on accelerometer fitted mountain lions that exhibited low acceleration during 'the pre-kill phase'(i.e. ambushing or waiting for prey) (Williams *et al.*, 2014). As leopards also primarily rely on such techniques to hunt and subdue prey, it may be that such low activity levels in heavily forested and sloped areas are partially explained by having to remain relatively still while hunting in areas that exhibit not only a sufficient amount of prey, and hunting coverage.

Additionally, a common behaviour amongst carnivores is to seek out safe habitats as a means to avoid intraguild, intraspecific, and anthropogenic threats in order to engage in vital behaviours such as cub rearing or resting (Pettorelli *et al.*, 2009; Martin *et al.*, 2010; May *et al.*, 2012; Oriol-Cotterill *et al.*, 2015). As leopard activity levels significantly decrease during the hottest part of the day, it is also possible that forested and sloped areas provide cooler refuge. While these areas may increase hunting success, lower activity levels therein may also result from leopards being able to conceal themselves while feeding or resting without interruption from larger carnivores (in this case, other leopards) as well as anthropogenic factors such as vehicles, humans, and domesticated dogs. Such results may also explain why leopard activity levels were significantly lower as distances to human infrastructure Increased.Although leopards are more likely to be inactive away from man-made structures (both on and off the mountain), subsequent analysis showed that leopards that went into agricultural, pastoral, and residential areas were significantly more active at night compared to those on the mountain (Figure 4.3). Leopards that went off the mountain supressed their diurnal activity.

While it is possible that higher activity levels in low lying areas may be due to other factors including moving through less densely vegetated and topographically complex terrain, given the relatively high mortality rates found in leopards in western Soutpansberg (Williams *et al.*, 2017), as well as the open hostility that many land owners have towards leopards (Chase Grey, Bell and Hill, 2017), it is conceivable that such activity levels may also reflect leopards moving more quickly through an environment that they perceive to be riskier. The notion that leopards may be aware of the risks involved with venturing

near human settlements is also exemplified by the analysis conducted in my previous chapter (Chapter 3) which found that leopards avoided establishing home ranges near human settlements despite the fact that such areas would otherwise provide suitable habitats.

Although temporal avoidance of dominant predators through altering activity levels has been recorded in smaller carnivore species (Durant, 2000), similar strategies have also been seen in larger carnivores inhabiting areas that are close to humans (Oriol-Cotterill *et al.*, 2015). As such, the results from this analysis show that leopards exhibit similar activity patterns as seen in other carnivore populations by reducing diurnal activity levels (while increasing nocturnal activity) when in close proximity to humans (Boydston *et al.* 2003 Carter *et al.* 2015 Ordiz *et al.* 2011 Valeix *et al.* 2012).

Overall, focal individuals that ventured off the mountain (N= 7) did so approximately 38% of the time throughout the study period. The fact that these leopards did not fully avoid anthropogenic habitats, but simultaneously modified their activity levels, suggests that although they perceive such areas as risky, the prevalence of both naïve and wild prey may outweigh the cost of complete avoidance.

The use of both GPS collar fixes and accelerometers allowed me to reveal complex trends regarding spatial-temporal variability in activity patterns in leopards. Having a greater understanding of the variability of activity patterns has the potential to not only identify areas that may be seemingly important for the focal species, but can potentially explain long term changes in population dynamics (Ripple *et al.*, 2014). My results have the potential to help understand the rapid decline in leopards in the Soutpansberg (Williams *et al.*, 2017), but also provide suggestions to mediate such a decline. The habitats where leopards have lower activity patterns (and are likely to be important rest sites) are the same areas where they prefer to establish home ranges (highly vegetated, topographically complex areas) that are characteristic of the southern portion of the western Soutpansberg Mountains (Chapter 3). Conservation efforts should to be prioritised in protecting habitats such as the northern mistbelt

forest. By doing so, would not aid in the survivability of leopards but also their primary prey.

Finally, understanding the temporal activity patterns of leopards off the mountain has the potential to help reduce human-carnivore interactions directly outside of the Soutpansberg Mountains. The results from my analysis show that when leopards that go off the mountain they are primarily nocturnal. One possible solution to mitigate conflict is to use such findings to assist in livestock management. For example, corralling domestic species at night may potentially minimise the risk imposed by leopards and other nocturnal carnivore species (Chase Grey, Bell and Hill, 2017). This may not only prevent livestock losses, yet may also allow for the coexistence between humans, and a dwindling leopard population.

Chapter 5: Foraging in Fear: Spatial Variation in Range Use, Vigilance, and Perceived Risk in Chacma Baboons (*Papio ursinus*)

Abstract

Animal space use patterns are influenced not only by resource acquisition but also the risk imposed by potential threats. Spatial variation in predation risk can lead to behavioural modifications ranging from increased vigilance to spatial avoidance to alleviate such risks. With the aid of spatial autoregressive models, I determined if perceived risk in chacma baboons was influenced by the probability of encountering leopards or intergroup encounters. I also assessed whether long term annual and seasonal space use was influenced by both the distribution of resources and the probability of encountering threats. Finally, I assessed whether vigilance varied spatially in response to not only potential threats, but also on the periphery of their home range. Results demonstrated that perceived risk in baboons is primarily related to intergroup encounters rather than predators. Baboons annually and seasonally modified their range use in relation to the probability of intergroup encounters. Vigilance rather than avoidance was found to be the main antipredator strategy when faced with the probability of encountering leopards. These results highlight that other baboon groups, rather than predation have a bigger influence on space use in baboons. In addition, I found that baboons use different long term strategies to alleviate the risk to baboons imposed by different threats.

5.1 Introduction

Non-sedentary animals move throughout their environment (i.e. home range) in order to acquire essential resources (i.e. foraging and reproductive opportunities) (Mosser *et al.*, 2014). While doing so, animals may utilise their spatial memory to safely manage the acquisition of resources while simultaneously avoiding the risk associated with predation and/or interspecific competition (Fagan *et al.*, 2013). Animals may trade off energy gains from foraging in food rich yet potentially risky areas as a means to prevent predation (Lima, 1998b). In addition, animals may invest in costly antipredator

behaviours such as vigilance or alarm calling when traversing through areas that are perceived to be dangerous to alleviate risk (Brown and Kotler, 2004; Creel and Christianson, 2008; Laundré, Hernández and Ripple, 2010). Understanding how animals behaviourally respond under both the risk of predation and interspecific competition while simultaneously maintaining resource acquisition has the potential to provide valuable information on animal decision making processes and to movement ecology more generally.

Space use patterns are often driven by the distribution of essential resources such as food, water, and in some species, the location of refuges such as burrows or sleeping sites (Mysterud and Ims, 1998; Manly *et al.*, 2002). In addition, space patterns may also be driven by social factors such as the search for mates and territorial defence (Burt, 1943; Mills, 1983; Lehmann *et al.*, 2008; Markham *et al.*, 2013). Many animal often restrict their movement patterns to a distinct area on the landscape that contains the requirements needed to maintain fitness levels (i.e. a home range) (Burt, 1943; Powell and Mitchell, 2012).

One of the most prominent factors that influences an animal's space use is the variable levels of perceived risk that they experience due to the presence of threats, from predators. Coined 'the landscape of fear', perceived predation risk may not necessarily be homogeneous throughout the landscape yet can be viewed as "peaks and valleys", with some areas considered relatively safer than others (Laundré, Hernandez and Ripple, 2010). For example, areas of dense vegetation that are beneficial for a hunting predator and so may be perceived as riskier compared to areas that provide efficient escape routes and greater visibility. Given such risks, prey should choose to forage in areas where risk from predation is low, even if that requires a trade off in food abundance or quality (Edwards, 1983; Sih, 1984). In contrast, in habitats where the risk from predation is relatively constant throughout the landscape and avoidance is near impossible, prey may have little choice but to feed at such optimal foraging sites, and develop other traits (such as vigilance) to mediate risk (Schmidt and Kuijper, 2015).

Despite being one of the most well studied mammalian taxa, there have been few studies on how perceived risk influences spatial patterns in primates. This is especially surprising since most primate species (including the largest) have been recorded predated on (Isbell, 1994; Hart, 2007) and the importance that predation may have had on primate evolution and behavioural ecology (Isbell, 1994; Hill and Lee, 1998; Treves, 1999; Boinski, Treves and Chapman, 2000; Zuberbühler and Jenny, 2002).

Willems and Hill (2009) and Coleman and Hill (2014) assessed how perceived risk influenced space use by semi-terrestrial vervet monkeys and arboreal samango monkeys *(Cercopithecus albogularis schwarzi*) , respectively, in the Soutpansberg Mountains, South Africa. Perceived risk on space use varied dramatically between the two species with the perceived risk of arboreal predators such as eagles having a greater influence on space use in samango monkeys compared to terrestrial predators (Coleman and Hill, 2014) while space us in vervet monkeys was negatively influenced by the perceived risk from terrestrial predators such as baboons and leopards, with aerial predators having no effect. In both cases, the landscape of fear had greater effect on space use compared to food availability, highlighting the importance of the landscape of fear.

Ranging throughout most of southern Africa, chacma baboons (*Papio ursinus*) live in large, complex, groups that contain both multiple males and females (Barrett and Henzi, 2008). Like other primate species, home ranges in baboons are often constrained to areas that contain essential resources such as water, food availability, and sleeping sites (Altmann and Altmann, 1973) and home range size, as well as day journey length, are dependent on the spatial distribution of such resources (Cowlishaw, 1999).

In addition to the availability of essential resources, several studies have also shown that baboon range use may also be affected by predation risk. Cowlishaw (1997) found that baboons in Tsaobis Leopard Park, Namibia were more likely to forage and engage in activities such as grooming in habitats that are perceived to be safer from predation (i.e. greater visibility). In addition, similar patterns of habitat avoidance in areas exhibiting lower visibility has also been

found in yellow baboons (*Papio cynocephalus*) in Amboseli National Park, Kenya (Altmann, 1974). Such avoidance of areas with lower visibility may likely be explained by the fact that baboons are primarily vulnerable to predators (such as large felids) that rely on stealth to ambush prey. Although baboons are occasionally predated on by lions (*Panthera leo*) (Busse, 1980), most recorded predation events have been by leopards, who not only have the ability to hunt baboons during the day, but pose a threat at night due to their ability to access sleeping sites (Altmann and Altmann, 1973; Busse, 1980; Cowlishaw, Behaviour and Dec, 2015; Matsumoto-Oda, 2015; Isbell *et al.*, 2018). As such, although baboons are generally not considered to be a large part of the diet of leopards (Hayward, Henschel, O'Brien, Hofmeyr, Balme and G. I.H. Kerley, 2006) (but see (Jooste *et al.*, 2013)) they may still pose a great enough threat to be avoided (Altmann and Altmann, 1973).

In addition to both predation and the availability of resources, space use in baboons may also be influenced by other groups. Chacma baboons are not known to be completely territorial, and as such, home ranges between groups have the potential to substantially overlap with one another. Intergroup interactions have been shown to more likely occur on home range boundaries and in the presence of essential resources (such as food or water) (Cowlishaw, 1995) and have been observed to vary considerably between tolerance and aggression, with some encounters having been fatal (Shopland, 1982).

Although intergroup encounters often occur in areas exhibiting the presence of essential resources, Cowlishaw (1995) found that the quality and availability of such resources did not necessarily influence the magnitude of aggression between chacma baboon groups in Namibia. Instead, he suggested that aggressive and competitive behaviours between different groups (i.e. aggression, female herding, and infanticide) may represent male reproductive tactics for defending prospective mating opportunities. Kitchen and colleagues (2004) found that chacma baboons residing in Okavango Delta (Botswana) were more likely to engage in aggressive or competitive intergroup encounters when oestrous females were present (Kitchen, Cheney and Seyfarth, 2004)

Markham (*et al.,* 2013) found spatial avoidance may act as a strategy to minimise reproductive opportunities in competing groups. Avoidance and overlap in neighbouring yellow baboon groups in the Amboseli Basin (Kenya) varied considerably over different time scales (weekly, bi-weekly, and monthly) with baboon groups more likely to overlap with one another when feeding. In contrast, the probability of overlap decreases as the numbers of fertile females increased (Markham *et al.*, 2013), suggesting that short term avoidance in baboons was most likely in response to reproductive strategies than resource displacement. This analysis did not consider, however, how baboons balance food acquisition and predator avoidance while simultaneously avoiding the risk imposed by other groups.

Animals have also been found to use vigilance to detect potential threats, with the proportion of time an animal spends vigilant reflecting their susceptibility to predation (Mooring *et al.,* 2004). Vigilance has thus been a useful tool in assessing perceived risk (Lima and Dill, 1990; S. Lima and Bednekoff, 1999). Given that predation risk may vary considerably across habitat types, vigilance levels have been found to vary spatially throughout the landscape. Increased vigilance levels in response to heightened predation risk have been found in numerous mammalian taxon including elk (Creel *et al.*, 2005; Liley and Creel, 2008), big horn sheep (*Ovis canadensis*) (Mooring *et al.,* 2004), squirrels (*sp.)* (Arenz and Leger, 2000; Makowska and Kramer, 2007), and even brown bears (*Ursus arctos*) (Nevin and Gilbert, 2005). Increased vigilance has also found to vary in prey items in response to the hunting method utilised by the predator. For example, Makin (*et al.,* 2018) found that ungulates such as warthog, gemsbok, and red hartebeest significantly increased their vigilance levels when faced by the risk imposed by ambush predators such as lions compared to cursorial predators such as African wild dogs (*Lycaon pictus*) or cheetahs (*Acinonyx jubatus*). Such variable behavioural responses between predator hunting types may be due to the fact that heightened vigilance (and thus early detection) may not necessarily be useful when faced with predators that rely on chasing and subsequently, 'testing' their prey, rather than ambushing (Makin, Chamaillé-Jammes and Shrader, 2018). In addition to predation, vigilance levels in animals have been shown to increase when faced with intraspecific threats.

For example, impala (*Aepyceros melampus*) have been found to increase their vigilance levels towards conspecifics when faced with a perceived change in resource abundance (Smith and Cain, 2009).

Vigilance in primates has been found to serve multiple functions ranging from predator detection (Cords, 1995; Rose and Fedigan, 1995; Cowlishaw, 1998; Coleman, 2013), intraspecific threat detection (Steenbeek *et al.*, 1999; MacIntosh and Sicotte, 2009), to social monitoring (Hirsch 2002; Gaynor and Cords 2012). In addition, primate vigilance levels have been shown to also vary both vertically and horizontally throughout space. For example, vigilance has been shown to decrease when higher in the canopy in brown capuchin monkeys (*Cebus apella*) (Hirsch 2002), white colobus monkeys (*Colobus vellerosus*) (MacIntosh and Sicotte, 2009), wedge capped capuchin monkeys (*Cebus olivaceus*) (De Ruiter, 1986), and blue monkeys (*Cercopithecus mitis*) (Gaynor and Cords, 2012). Being on the ground exposes primates to threats from terrestrial predators such as snakes or felids and may offer fewer escape options. Interestingly**,** De Ruiter (1986) found that wedge capped capuchin monkeys scanned less when actually on the ground, which may be due to an increase in foraging opportunities.

Although prey species may be most often at risk from ambush predators in areas exhibiting limited visibility (such as increased foliage density), several studies show that habitat characteristics may either have no effect (Alberts, 1994; Hill and Cowlishaw, 2002) or lead to a decrease in primate vigilance (Gaynor and Cords, 2012). Although increased vigilance in areas exhibiting lower visibility (due presumably to predation risk) is found in other taxa, it has been hypothesed that the opposite effect found in many primates may be due to the fact that habitats exhibiting greater visibility may also allow primates to visually scan more of their environment (Gaynor and Cords, 2012).

Vigilance levels in primates can be influenced by intergroup relationships (MacIntosh and Sicotte, 2009; Busia, Schaffner and Aureli, 2016). Although vigilance levels have been recorded to increase during direct interactions (MacIntosh and Sicotte, 2009), they also has the potential to increase in areas where intergroup encounters are more likely. For example, black and white

colobus monkeys are likely to increase their vigilance in areas where substantial overlap occurs between groups. (MacIntosh and Sicotte, 2009). They also found that the increase in vigilance rates regardless of whether there was an encounter or not, suggests that the probability of an interaction alone is enough to cause an increase in vigilance (MacIntosh and Sicotte, 2009). Additionally, spider monkeys (*Ateles geoffroyi*) increased their vigilance on the periphery of their home range (Busia, Schaffner and Aureli, 2016). In this instance, an increase in vigilance may be due to not only the probability of encountering other groups, yet also the potential risks associated with traveling through relatively unused areas (i.e. predation risk).

Although Willems (2008) and Coleman (2013) assessed the landscape of fear in vervet and samango monkeys (respectively) by recording and assessing where predator specific alarm calls are more likely to be elicited, it should be noted that these studies did not assess where the predators are likely to be encountered, and if perceived risk in these primates is directly influenced by the probability of encountering their predators. By assessing the spatial perception of risk exhibited by the primates alone, they could not determine whether such responses are also a reaction to actual risk. Given such limitations, I opted to integrate the results pertaining to my previous analysis on 3rd order leopard resource selection functions (Chapter 3) to determine whether the spatial and behavioural responses exhibited by baboons can be explained by the probability of encountering leopards within their home range. The incorporation of carnivore data when assessing spatial variation in range use and vigilance provides an exciting and important opportunity when attempting to address whether perceived risk in primates can be directly explained by the probability of directly encountering their primary predator, or, whether perceived risk can be explained by other factors.

I hypothesised that the probability of encountering leopards (H1) and the probability of encountering other baboon groups (H2) would have a significant impact on space use of chacma baboons in the western Soutpansberg Mountains.

In contrast, I hypothesise that overall, baboon range use will be positively and significantly influenced by areas exhibiting higher food availability (H3) but that baboons may trade off safety with the abundance of food (H4). As the western Soutpansberg has a seasonal environment with fluctuating levels of food availability (Willems, Barton and Hill, 2009), I explore whether the risk-foraging trade-off varies seasonally.

I also hypothesised that vigilance should increase in areas where the probability of intergroup encounters increases (H5) as well on the periphery of their home range (H6). Finally, I predicted that baboons will behaviourally respond to increased predation risk by heightening vigilance levels in areas where the probability of encountering leopards increase (H7).

5.2 Methods

5.2.1 Study Site

Data were collected in the western Soutpansberg Mountains (Limpopo Province, South Africa) (central coordinates: 23°06'45.14"S 29°11'37.10"E). The Soutpansberg Mountains run roughly 250 km from east to west as well as 15-60 km from north to south and has a maximum elevation of 1758 metres, with the highest peak, Mt. Lajuma, located at the study site (Section 2.2).

Currently, the only large carnivore species that still reside in the western Soutpansberg include the brown hyaena (*Hyaena brunnea*) and the leopard (Chase Grey, 2011), with the latter having been recorded predating on primates including chacma baboons (Chase Grey, Bell and Hill, 2017).

5.2.2 Home Range Analyses

Data utilised for this analysis derived from a habituated chacma baboon group between the years 2014 and 2017. I used coordinates that were collected every twenty minutes on Garmin GPS devices by Primate Predator Project (PPP) staff and assistants before every behavioural scan for all home range analyses. Before calculating home ranges for each year, all individual scan points (N=6890) were checked for geographical errors (i.e. individual points that were clearly out of range). Following, Local Convex Hulls analysis (T-LoCoH) (Lyons, Turner and Getz, 2013a) was used to calculate home range and space use

intensity for each year individually at 99% isopleths. LoCoH analysis was chosen over kernel density estimation (KDE) for this specific analysis due to its superior ability to not only define hard boundaries (such as cliffs), but also to be able to better handle clumped or overlapping points (Ryan, Knechtel and Getz, 2006; Getz *et al.*, 2007; Scull *et al.*, 2012; Signer *et al.*, 2015). These were characteristic of the dataset due to repeated scans at common locations such as sleeping sites.

The *a* (Adaptive) method was employed for the construction of home ranges due to its ability to construct smaller hulls in clustered regions (Getz *et al.*, 2007; Lyons, Turner and Getz, 2013a, 2013b), which in turn provides a more comprehensive output in areas that are utilised more frequently.

Utilisation distribution polygons were uploaded into ArcGIS (10.3.1) and transformed into yearly rasters. Values were inverted to ensure higher values reflected intensively used areas (Appendix 4; Figures S4.5 and S4.8) and then the cell statistics tool in ArcGIS was used to combine all yearly UDs thus allowing for the creation of a raster which represents the utilisation distribution for focal baboons throughout the entirety of the study period (Figure 5.1). The creation of seasonal utilisation distributions used similar methods by combining May to August for winter and November to January for summer) (Appendix 4; Figures S4.9 and S4.10).

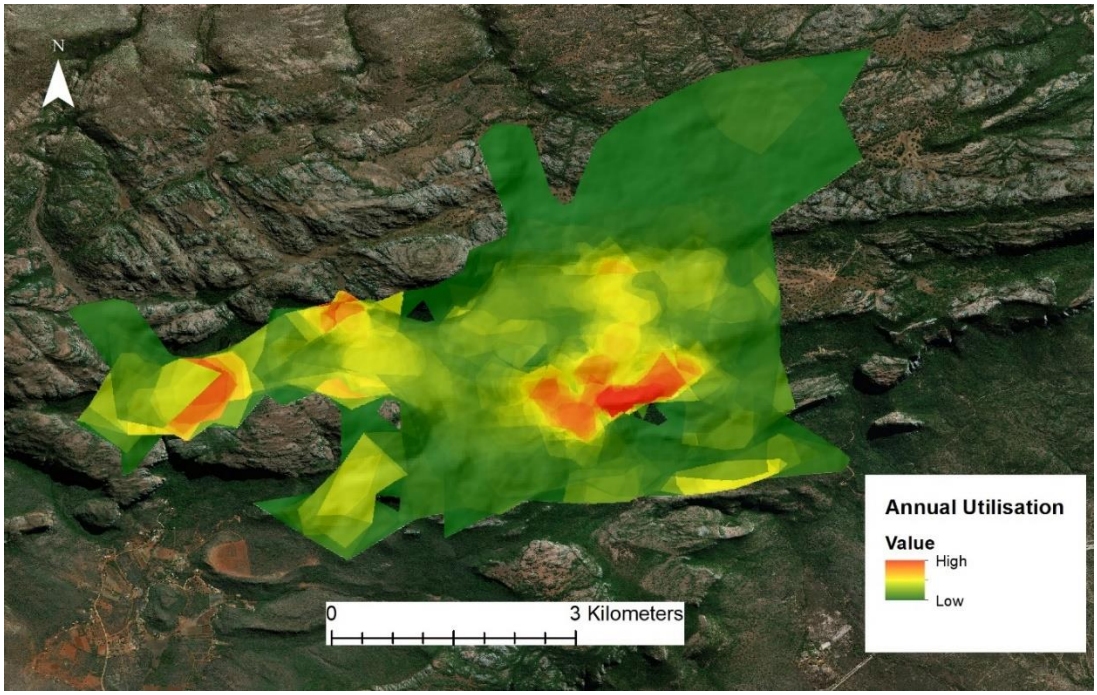

Figure 5.1 Annual utilisation distribution of focal baboon group between 2014-2017.

Table 5.1 Annual information regarding home range size and number of scans per year.

Year	Start/End Dates	Number of Scans	Furthest Distance Between Points (metres)	99% Home Range Size (square kilometres)
2014	15-04-2014 to 13-12-2014	950	9078	14.76
2015	21-01-2015 to 22-10-2015	1403	8254	13.42
2016	06-01-2016 to 17-11-2016	2486	10487	17.29
2017	13-01-2017 to 21-09-2017	2051	7025	14.25

5.2.3 Landscapes of Fear

Although chacma baboons do not necessarily make predator-specific alarm calls, baboons do exhibit variation in alarm call type depending on age and sex (Fischer, Hammerschmidt, *et al.*, 2001; Fischer *et al.*, 2004). For example, females (and juveniles) elicit high shrill barks when encountering predators (regardless of the predator species) (Fischer, Hammerschmidt, *et al.*, 2001), whereas males respond by producing loud two-syllable barks known as 'wahoos' (Fischer *et al.*, 2002). In addition, the 'wahoo' call produced by males' functions not only as an anti-predator defence, but also as a response to intra and intergroup aggression and competition between other males. While alarm calls are often produced during direct encounters (Fischer *et al.*, 2004; Kitchen, Cheney and Seyfarth, 2004), several studies have found that baboons, like other primate species (Willems, Hill and Willems, 2009; Coleman and Hill, 2014) are also likely to produce alarm calls while in areas that are perceived to be riskier (Altmann and Altmann, 1973; Cowlishaw, 2010). As a result, it is possible to generate a landscape of fear for baboons based off on vocalisations to assess whether perceived risk influences spatial distribution.

Both alarm calls and wahoos deriving from adult baboons collected by PPP staff and assistants during the study period (15-04-2014 to 20-09-2017) were used generate the risk maps. Alarm calls and wahoos were first visually inspected for any geographic or data entry errors and then combined for each year. All alarm calls and wahoos that were directly prompted due to encountering domesticated dogs (*Canis lupis familiaris*) and vehicles were omitted from this analysis. Alarm calls and wahoos were combined into the same dataset because it was generally not possible for the observer to determine the exact cause of the call and any alarm call, regardless of the specific context, can be interpreted as a measure of risk.

Gaussian kernel density estimates (KDEs) were used to assess the yearly distribution of alarm calls in Geospatial modelling environment (Beyer, 2012). I used the PLUGIN bandwidth (Gitzen, Millspaugh and Kernohan, 2006) since it not only provided more reasonable and consistent outputs across all four years by not over or under smoothing, but has also been shown to outperform LSCV

in studies where points are very clustered (Gitzen, Millspaugh and Kernohan, 2006; Walter *et al.*, 2011; King *et al.*, 2016; Tri *et al.*, 2016) or on the periphery (McGeachy, Hamr and Mallory, 2017). Using the raster calculator tool in ArcGIS, yearly KDEs were divided by their corresponding utilisation distributions in order to create annual landscapes of fear. Finally, the cell statistics tool in ArcGIS was used merge all yearly landscapes of fear while retaining the mean for overlapping areas in order to obtain a layer that represented perceived risk over the study period (Figure 5.2).

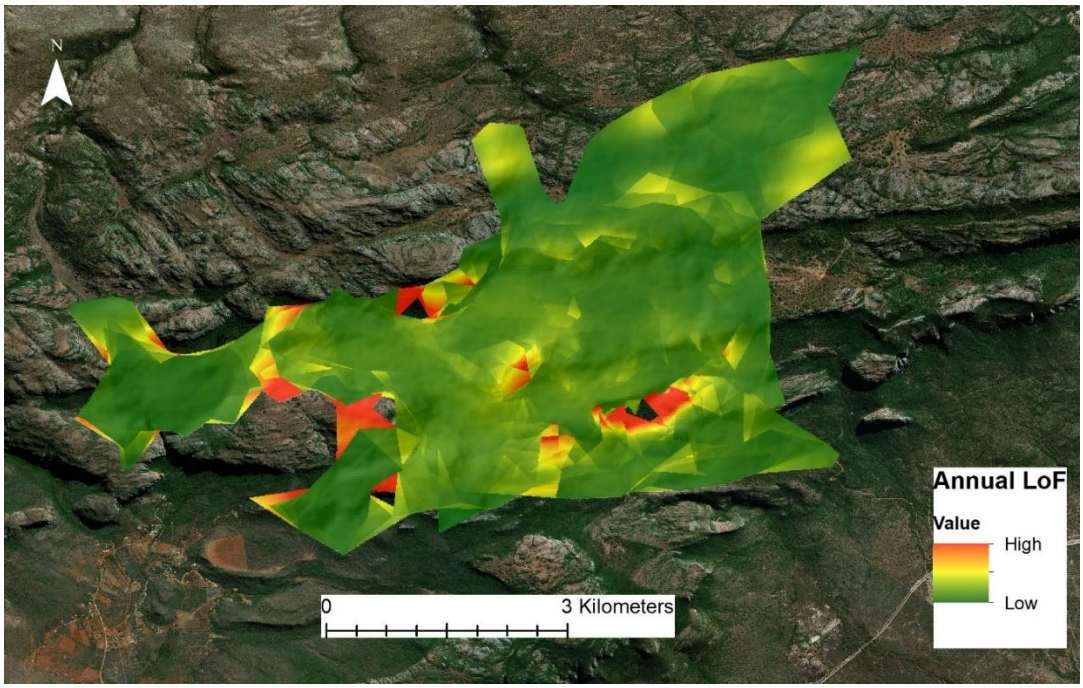

Figure 5.2 Map representing the annual probability for chacma baboons to elicit vocalisations throughout their home range.

5.2.4 Intergroup Encounters

Intergroup encounters recorded *ad libitum* from 2014-2017 (N=108) by PPP staff along with the utilisation distribution were used to create a spatial layer that represented the probability of an intergroup encounter. All recorded intergroup encounters were inspected for errors, and then uploaded by year into GME. I chose the PLUGIN bandwidth for the creation of KDE's due to relatively small sample sizes and several instances of point clustering (Gitzen, Millspaugh and Kernohan, 2006; Walter *et al.*, 2011; King *et al.*, 2016; Tri *et al.*, 2016). Each annual intergroup KDE was divided by their corresponding utilisation distribution to create annual intergroup probability layers. Lastly, all

annual intergroup probability layers were merged with the cell statistics tool within ArcGIS to create a probabilistic landscape of intergroup encounters that encompassed the entirety of the study period while simultaneously retaining the mean for all overlapping years (Figure 5.3). These same methods were also utilised for the creation of seasonal intergroup encounter layers (Appendix 4; Figures S4.11 and S4.12).

5.2.5 Leopard Resource Selection Functions (RSFs)

In chapter 3, I assessed the probability of occurrence (RSF) for leopards within the western Soutpansberg on three different spatial scales: where leopards are likely to establish home ranges (2nd order RSF), where they are likely to occur within their home ranges (3rd order RSF), and where they are likely to hunt and kill their prey (4th order RSF) (Johnson, 1980). The projection from the 3rd order RSF was selected for the current analyses as all of the leopards utilised in the study shared overlapping home ranges with the focal baboon group, and as a result, areas preferred by such individuals on a localised scale were also most likely to also represent areas where baboons are more likely to encounter leopards.

Third order resource selection functions were created through a used/available design where collared leopard GPS fixes (N= 7576) were paralleled to an equal number of generated points that were randomly distributed throughout each individual home range (Section 3.2.5). The top candidate 3rd order RSF model was selected by AIC through the use of the Mumin package in R (Barton, 2015) with normalized difference vegetation index (NDVI) and distance from human settlements having positive and significant effects on the probability of leopard occurrence. The raster calculator (ArcGIS) was used to calculate and spatially project the top 3rd order resource selection function model (Figure 5.3). To improve visual interpretation, linear stretching was applied to the resulting raster projection and were scaled to values between 0 and 1 (Johnson, Seip and Boyce, 2004). See chapter 3 for further details.

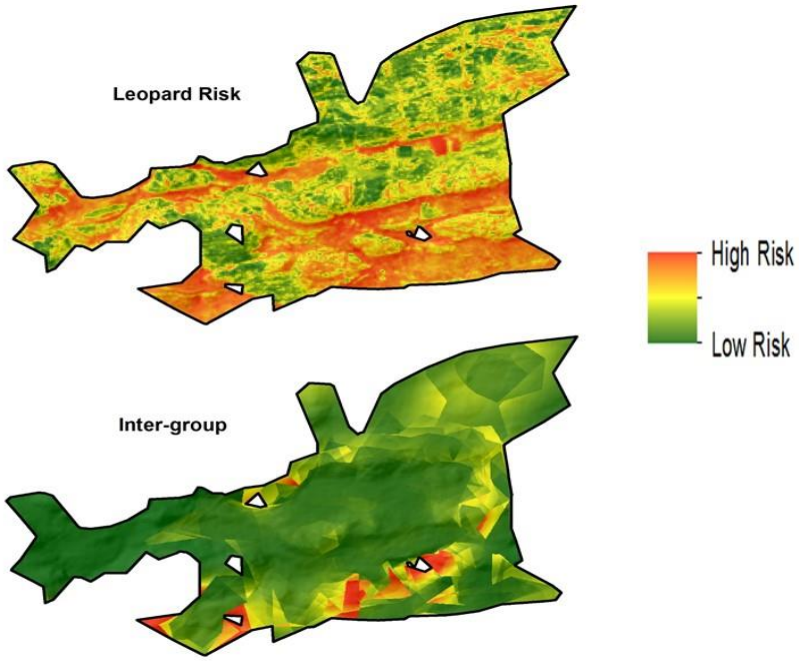

Figure 5.3 Risk maps representing the probability of encountering other baboon groups or leopards.

5.2.6 Environmental Variables

Waterway data were created with the aid of the Optimized Pit Removal Tool extension (Centre for Research in Water Sources, Austin, TX) and then converted into a Euclidean distance raster in ArcGIS. (Figure 5.4). Sleeping sites (N= 34) recorded by PPP staff and assistants were uploaded as point shapefiles in ArcGIS and the Euclidean distance tool in ArcGIS was used to create distance from sleeping site layers. (Figure 5.4)

Phenological and vegetation quadrat data collected by PPP staff and assistants between 2014 and 2017 were used to assess fruit availability throughout the entirety of the baboons' home range. Vegetation quadrat data (N= 905) consisted of randomly generated points that were distributed in an area that overlapped with all three diurnal primate species (baboons, samangos, and vervets). Vegetation sampling in 5m x 5m quadrats collected visibility, number of trees and saplings and percentage cover. All tree species found within the quadrat were identified, along with their corresponding DBH (diameter at breast height), height, and crown diameter measurements.

Only tree species constituting 5% or more of the baboons' diet were included in analysis. Given the small number of plant species included at this threshold on an annual basis (N= 4), I also included all species consumed in winter and summer which exceeded the threshold resulting in 12 species overall.

A simple linear regression was used to determine a correlation between crown height with average fruit availability for each tree species deemed important for consumption. Crown height was deemed to be an important predictor in determining whether trees bore fruit or seeds across taxa, and scatterplots were created in GGplot2 (Wickham, 2009) as a means to visually explore cut off points, with trees below a certain threshold being excluded from averaging total food availability. Trees that did not bear fruit were assigned a zero when applied towards food availability across all habitats.

All fruit and seeds from food bearing trees averaged on an either an annual (throughout the study period) or seasonal level. Fruit and seed diameters were obtained from Palgrave (1996) and the volume of an ellipsoid was used in order to obtain food volume per tree species:

$$V = \frac{4}{3}\pi\ abc$$

In this instance, V represents the volume where a, b and $c$are the radiuses of the fruit or seed (obtained through the diameters). The formula used for flowers represented the volume for a half ellipsoid:

$$V = \frac{2}{3}\pi\ abc$$

Fruit and flower availability across species were calculated by multiplying fruit volume by average number of fruit (or flowers) on either an annual or seasonal level, whereas seed availability was calculated by multiplying the average seed pod volume (seed volume multiplied by average number of seeds in a pod) by the average number of seeds per tree taxon.

Finally, the food availability data for highly consumed species were attached to all corresponding tree species (at or above the food bearing threshold) that

were recorded in the vegetation quadrats and summed to provide overall food availability per quadrat.

All quadratic points with assigned food values were then synced with habitat types derived from a categorical land coverage map of South Africa created by GeoTerraImage (Inc.) and accessed through the South African Spatial Data Infrastructure (Dept. of Rural Development and Land Reform, Republic of South Africa) website at http://www.sasdi.net/) that covers the entirety of the study site. Food availability for the study area (on both an annual and seasonal level) was finally obtained by averaging all quadratic points (with food availability values attached) found within each specific habitat type (Appendix 4; Figures S4.2-S4.4 and Tables S4.1-S4.3).

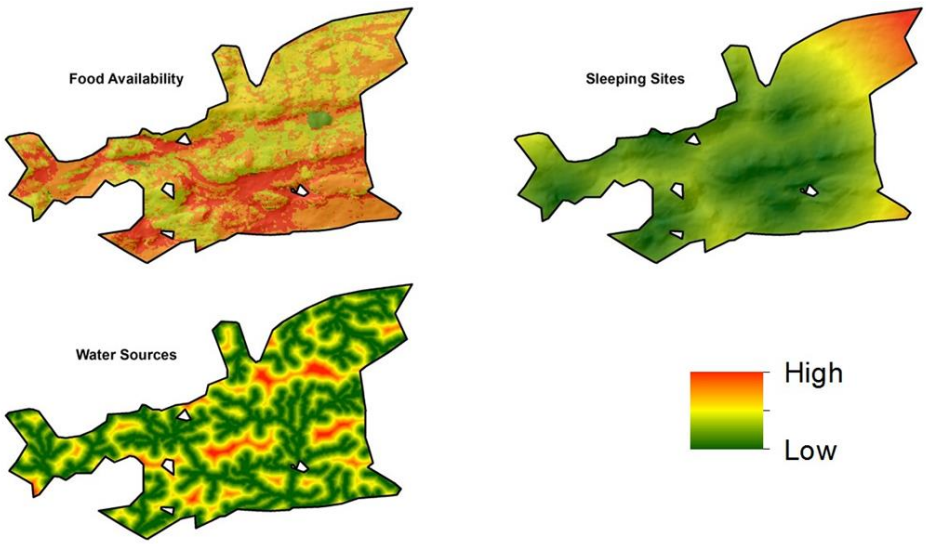

Figure 5.4 Annual distribution of food availability, water sources and sleeping sites.

5.2.7 Spatial Vigilance

Vigilance data were collected through instantaneous scan sampling by PPP staff and assistants between 2014 to 2017 (Section 2.4.2). For this analysis, vigilance was defined as any form of 'looking' where the focal baboon could visually detect stimuli from a distance, regardless of whether it was a potential threat or not (Allan and Hill, 2018). In contrast, non-vigilance in this analysis refers to when eyes are closed as well as any kind of looking where vision is clearly obstructed or visual stimuli from a distance cannot be observed because the animal is paying attention to a specific object (i.e. looking at a food item or

paying attention to a grooming partner). Overall 'looking' was selected to be the most appropriate indicator of vigilance for this analysis compared to traditional definitions (pre-emptive and reactionary) since the act of looking may be equally as efficient at detecting threats compared to being actively vigilant (Treves, 2000; Allan and Hill, 2018).

All scan data were manually inspected for any kind of geographical or data collection errors. Given sex differences in vigilance (Cheney and Wrangham, 1987; Cowlishaw, 1998), I used vigilance data from adult females only for this analysis (Hill and Cowlishaw, 2002). I used the percentage of female baboons vigilant per scan by dividing the number of vigilant individuals by the total number of scans (De Ruiter, 1986; Isbell and Young, 1993b). Only scans that contained five females or more were included into the final vigilance dataset so that proportions were not biased by values derived from small sample sizes.

5.2.8 Statistical Analysis

Five models (through four datasets) (Appendix 4; Table S4.4) were used to fully address landscapes of fear and vigilance in baboons. These four datasets varied primarily by variables utilised for analysis.

The first model (Model A; dataset A) was used to assess if the perceived risk (through alarm calls), as well as the distribution of essential resources were primary drivers of range use in baboons in the western Soutpansberg Mountains.

The second model (Model B; dataset A) assessed if perceived risk in baboons (through alarm calls) was driven by either intergroup encounters or the probability of encountering leopards. Model C assessed if predation risk, intergroup encounters, and food availability influenced range use in baboons.

As the western Soutpansberg experiences seasonal fluctuations in food availability, I assessed whether specific variables influenced range use during the peak of either summer (Model D; dataset B) or winter (Model E; dataset C) months. For each seasonal model, 1000 points were randomly generated across the home range. Food availability, as well as distance from sleeping sites and water, were used to assess if baboons seasonal range is driven by essential

resources. Additionally, the probabilities of encountering leopards as well as other groups were included in order to assess if seasonal range use was influenced by the avoidance of specific threats. The last model (Model F) consisted of proportion of individuals vigilant and was used to assess whether baboons exhibited spatial variation in vigilance.

For each model, 1000 points were randomly generated across the home range. Then, food availability as well as distance from sleeping sites and water were used to assess if baboons' seasonal ranges were driven by essential resources. Moreover, probabilities of encountering leopards as well as other groups were included in order to assess if seasonal range use was influenced by avoiding specific threats.

Spatial autocorrelation amongst variables can potentially lead to problems such as Type 1 Errors, when conducting analyses that have a spatial component (Dormann *et al.,* 2007). As such, all variables were independently inspected with the use of the univariate Moran's I tool in Geoda (Anselin, Syabri and Kho, 2006) to determine if spatial autocorrelation was present (Moran, 1950). Moran's I ranges between -1 and +1 with values of or near -1 representing negative spatial autocorrelation (perfect dispersion), value of or near 0 represents random dispersion (Ripa, 2000) and values close or at 1 signify high autocorrelation with perfect clustering (Ripa, 2000). All the variables displayed some level of spatial autocorrelation (Appendix 4; Table S4.4). and as such, models that accounted for spatial structure were favoured over traditional methods.

Spatial autoregressive models were used for models A-D to accommodate the spatial dependence found within and between observations (LeSage, 2008). Spatial autoregressive models are used to control for spatial auto correlation by taking the relationships between neighbouring values (through spatial weights) as well as a spatial autocorrelation parameter (ρ) into account, thereby allowing for spatial independence in the model residuals. Spatial autoregressive models have been shown to outperform traditional regression models which may not be able to control for spatial autocorrelation, thus leading to ambiguous results (Pace and LeSage, 2010).

To account for spatial autocorrelation, row standardised weight matrices ($\mathcal{W}$) set at the min-max distance (largest distance between neighbours) between all points were created in Geoda for each separate dataset. Inverse-distance based weights were specifically chosen over traditional distance based weight matrices due to the assumption that as distance increases, the similarity between individual points decreases (Thornton, Running and White, 1997).

After the construction of spatial weights, ordinary least squares (OLS) models were to assess the relationship between chosen predictors and response variables in a non-spatial context (Anselin, 1988). Although OLS models do not have a spatial component, they are typically regarded as a first step in any spatial analyses (Anselin, 1988).

Residuals from all OLS models were tested for autocorrelation using Moran's I (Appendix 4; Table S4.4). The presence of autocorrelation in the residuals for all OLS models suggested that a model that accounted for spatial structure would be more appropriate compared to standard regression.

I hypothesized that predictor values would only influence the response at a localised level, and as a result, the effect of X will only influence the values of neighbouring points of Y (local spillover effect) (LeSage, 2014). For example, a spatial point that is attributed to the higher probability of encountering leopards or other groups should not necessarily influence alarm call values at all other locations (global spillover). However, it is likely that a spatial point that is attributed to a higher probability of encountering threats *may* influence the alarm call patterns of neighbouring points.

To account for both spatial autocorrelation and local spillover between neighbouring points, a hierarchal modelling approach was utilised through the construction and analysis of three spatial models. Following Lesage and Pace (2014; 2009), these were the spatial lag of X model (SLX), spatial error model (SEM), and spatial durbin error model (SDEM).

The simplest of these models (SLX), can be considered to be an extension of a simple linear regression with the inclusion of spatially weighted independent

variables ($wx\theta$)(Lacombe, Holloway and Shaughnessy, 2014) and is expressed as:

$$y = X\beta + wx\theta + \varepsilon$$

Since the SLX model contains a spatial lag term, coefficients cannot be inferred as effects on the dependent variable. Instead, to account for autocorrelation, direct, indirect, and total effects are used to interpret results. Direct effects simply represent the impact on a predictor on its outcome (and are like traditional regression interpretation), whereas the total effect is the change in response to the direct impact and neighbour spillovers. Finally, indirect (spatial) impacts represent the spatial spillover between neighbours, and represents the difference between the total and direct impacts (LeSage and Pace, 2009).

An SEM model follows the formula derived from an OLS regression with the inclusion of vector of autocorrelated disturbance (u), an error term (ε) as well as autocorrelation parameters (λ) for the error (Wegener, 2014) and is expressed as:

$$y = X\beta + u$$

$$u = \lambda Wu + \varepsilon$$

Spatial error models assume that spatial dependence can be attributed to the error term (Wu) within the model, which is most likely to occur if spatial autocorrelation cannot be directly explained by the predictor variables included.

Finally, the spatial durbin error model (SDEM) incorporates spatial dependence in predictor variables (but not in the response) by including a spatial lag in the error term. The SDEM model is expressed as:

$$y = X\beta + Wx\theta + u$$

$$u = \lambda Wu + \varepsilon$$

Like the SLX model, the SDEM model is considered appropriate for localised analyses by incorporating the term θ, and thus allowing for localised spillover

effects that only impact immediate neighbouring points (LeSage and Kelley Pace, 2014). However, unlike the SLX model (which only includes spatially lagged predictor variables ($Wx\theta$), the SDEM model also includes spatially lagged error terms (Wu) (Gaughan, Gravelle and Siciliani, 2015; Burridge, Elhorst and Zigova, 2016).

5.2.9 Model Selection for Datasets A-D

Several decision-making processes were undertaken in order to determine whether the appropriate model should be reduced from a SDEM to a simpler spatial model (SEM, SLX).

Akaike Information Criterion (AIC) was used to rank all models created. In all cases, higher order spatial models such as the spatial error models and the spatial durbin error model had lower AIC compared to the simpler SLX model, as well as the non-spatial OLS. Following LeSage and Pace (2009), Likelihood-ratio tests were used to assess if top models (through AIC) should be restricted to a simpler model (Table 5.2). In all instances, a spatial durbin error model or a spatial error model were found to be the most appropriate for analysis.

Table 5.2 AIC values for all competing models per analysis.

Analysis	OLS	SLX	SEM	SDEM
Vocalisations (Model A)	-192.70	-192.49	-1271.43	-1282.94
Perceived Risk (Model B)	-936.26	-992.21	-2489.10	-2500.71
Annual Space Use (Model C)	-902.53	-970.09	-2358.87	-2397.86
Summer Space Use (Model D)	-779.69	-878.00	-3244.55	-3246.60
Winter Space Use (Model E)	-1298.75	-1308.98	-3109.51	-3149.73
Vigilance (Model F)	542.57	525.55	474.52	473.82

Then, the distributions of residuals for all top models were visually inspected for clustering in R studio. A Breusch-Pagan test was used to determine in model residuals had heteroskedasticity. While all models still exhibited some heteroskedasticity, this should not lead to bias in the coefficients (Romero and Burkey, 2011, Burkey, *personal communication*) and as a result, did not influence model selection.

5.3 Results

AIC values for all candidate models for assessing how perceived risk and resource distribution influenced space use (Model A) identified that the SDEM was the top candidate model compared to nested spatial models (SEM and SLX), as well as the non-spatial model (OLS). A likelihood ratio test confirmed that the SDEM was preferred over the restricted SEM model (likelihood ratio = -19.607 , $df = 4, p = 0.000$). As predicted, results derived from total impacts show a significant negative relationship between range use and the vocalisation landscape of fear (Table 5.3). Overall range use was not influenced by food availability, but baboons did choose to range within proximity to sleeping sites and water sources.

Table 5.3 Coefficients for baboon space use (as the dependent variable) in conjunction with perceived risk and distribution of sources (Model A; SDEM model).

Effects	**Estimate**	**Standard Error**	**Z value**	**Pr(>|z|)**
Direct				
Landscape of Fear	-2.711	2.306	-11.756	**<0.001**
Water Availability	6.749	3.395	-1.987	**0.046**
Sleeping Site	-1.271	3.672	-3.461	**<0.001**
Food Availability	2.347	3.431	0.068	0.945
Indirect				
Landscape of Fear	-2.471	0.007	-3.519	**<0.001**
Water Availability	-2.647	0.000	-2.611	**0.009**
Sleeping Site	-2.871	4.687	-0.612	0.540
Food Availability	9.323	0.000	0.080	0.936
Total				
Landscape of Fear	-5.183	0.007	-6.579	**<0.001**
Water Availability	-3.322	0.000	-3.010	**0.002**
Sleeping Site	-1.558	2.987	-5.216	**<0.001**
Food Availability	1.167	0.000	0.085	0.932

AIC scores found the SDEM model to be the top candidate model for determining how perceived risk (through alarm calls) are influenced by the

probability of encountering threats (Model B). In addition, a likelihood ratio test confirmed that the more complex SDEM model was preferred over the nested SEM (likelihood ratio test:$x^2 = 15.516, df = 2, p = 0.000$). The total impacts from the SDEM model show that the vocalisation landscape was positively related to intergroup encounters but there was no relationship with the probability of encountering leopards (Table 5.4). The direct and indirect impacts showed that baboons are not only likely to experience heightened perceived risk directly in areas where intergroup encounters are likely to occur (direct impact) but are also likely to do so when they are nearby such areas (indirect impacts).

Table 5.4 Coefficients for factors that influence the distribution for eliciting alarm calls (alarm call values as the dependent variable) (Model B; SDEM model).

Effects	**Estimate**	**Standard Error**	**Z value**	**Pr(>|z|)**
Direct				
Leopard	-0.008	0.608	-0.133	0.893
Intergroup	0.105	0.004	24.329	**<0.001**
Indirect				
Leopard	-0.253	0.179	-1.407	0.159
Intergroup	0.054	0.014	3.801	**<0.001**
Total				
Leopard	-0.261	0.206	-1.263	0.206
Intergroup	0.160	0.016	9.861	**<0.001**

Both AIC as well as a likelihood ratio test against the next candidate model (likelihood ratio test:$x^2 = -48.99, df = 5, p = 0.00000000223$), found the SDEM to be the most appropriate fit for determining how annual space use is influenced by resource distribution and the probability of encountering threats (Model C) (Table 5.5). Total impacts complement the two previous analyses and show that baboon range use is negatively and significantly influenced by the probability of encountering other groups while the probability of encountering leopards had no effect. Food availability had no effect on annual range use, but

baboons were more likely to range in proximity to both sleeping sites and water sources.

Table 5.5 Coefficients for variables that influence annual space use (annual space use value as the dependent variable) in chacma baboons (Model C; SDEM model).

Effects	Estimate	Standard Error	Z value	Pr(>|z|)
Direct				
Leopard	-0.050	0.045	-1.100	0.271
Intergroup	-0.036	0.002	-14.619	**<0.001**
Water Availability	-0.000	0.000	-2.654	**0.007**
Sleeping Site	-10.011	3.869	-2.587	**0.009**
Food Availability	0.000	0.000	1.121	0.262
Indirect				
Leopard	-0.179	0.144	-1.240	0.214
Intergroup	-0.048	0.008	-5.515	**<0.001**
Water Availability	0.000	0.000	-2.823	**0.004**
Sleeping Site	4.905	4.905	-1.259	0.207
Food Availability	0.000	0.000	0.943	0.345
Total				
Leopard	-0.229	0.170	-1.345	0.178
Intergroup	-0.085	0.010	-8.506	**<0.001**
Water Availability	-0.000	0.000	-3.396	**<0.001**
Sleeping Site	-16.187	3.080	-5.255	**<0.001**
Food Availability	0.000	0.000	1.064	0.287

AIC scores for all candidate models found that an SDEM (Model D) performed better than nested spatial models (SEM and SLX) and non-spatial models for assessing space use in summer months. In addition, a log likelihood test found the SDEM to outperform the nested SEM (likelihood ratio test:$x^2 = -12.05, df = 5, p = 0.03411$) (Table 5.6). Total impacts for Model D found that summer range use in baboons was significantly negatively influenced by intergroup encounters, with distance to sleeping sites also significant.

Probability of encountering leopards, food availability and distance to water sources had no effect on baboon range use in summer.

Table 5.6 Coefficients for variables that influence summer space use (summer space use values as the dependent variable) in chacma baboons (Model D; SDEM model).

Effects	Estimate	Standard Error	Z value	Pr(>|z|)
Direct				
Leopard	0.015	0.024	0.626	0.531
Intergroup	-0.164	0.006	-23.553	**<0.001**
Water Availability	-0.000	0.000	-1.707	0.087
Sleeping Site	-8.020	2.637	-3.041	**0.002**
Food Availability	0.000	0.000	0.748	0.453
Indirect				
Leopard	0.044	0.085	0.514	0.606
Intergroup	-0.194	0.019	-1.544	0.122
Water Availability	-0.000	0.000	-0.927	0.353
Sleeping Site	-6.248	4.799	-1.301	0.192
Food Availability	0.000	0.000	1.980	**0.047**
Total				
Leopard	0.059	0.098	0.607	0.543
Intergroup	-0.194	0.021	-8.865	**<0.001**
Water Availability	-0.000	0.000	-1.371	0.170
Sleeping Site	-14.268	3.900	-3.658	**<0.001**
Food Availability	0.000	0.000	1.868	0.061

AIC scores found the SDEM to be the parsimonious model for winter range use (Model E). In addition, a likelihood ratio test found the SDEM to be more appropriate for interpretation compared to the nested SEM (likelihood ratio test:$x^2 = 50.221, df = 5, p =< 0.000$) (Table 5.7). As predicted, baboon range

use in winter months was significantly and negatively influenced by the probability of encountering other groups. Baboons also chose to utilise areas in winter months with a greater abundance of food. In addition, range use in winter was still influenced by distance to sleeping sites, but not by water.

Table 5.7 Coefficients for variables that influence winter space use (winter space use values as the dependent variable) in chacma baboons (Model E; SDEM model).

Effects	**Estimate**	**Standard Error**	**Z value**	**Pr(>|z|)**
Direct				
Leopard	0.015	0.030	0.512	0.608
Intergroup	-0.109	0.003	-27.641	**<0.001**
Water Availability	-0.000	0.000	-0.688	0.491
Sleeping Site	-12.587	3.191	-3.943	**<0.001**
Food Availability	0.000	0.000	0.112	0.910
Indirect				
Leopard	-0.026	0.142	-0.188	0.850
Intergroup	-0.050	0.009	-5.220	**<0.001**
Water Availability	-0.000	0.000	-1.364	0.172
Sleeping Site	2.506	6.336	0.395	0.692
Food Availability	0.001	0.000	2.548	**0.010**
Total				
Leopard	-0.011	0.153	-0.071	0.942
Intergroup	-0.159	0.011	-14.405	**<0.001**
Water Availability	-0.000	0.000	-1.529	0.126
Sleeping Site	-10.080	5.117	-1.969	**0.048**
Food Availability	0.001	0.000	2.340	**0.019**

AIC as well as a likelihood ratio test, found the spatial error model (SEM) to be a better fit over the more complex SDEM (likelihood ratio test:$x^2 =$

$-6.6922, df = 3, p = 0.082$) for determining if spatial vigilance is influenced by the probability of encountering potential threats as well as on the periphery of the home range (Model F; Table 5.8). As predicted, there was a highly significant and positive relationship between baboon vigilance and the probability of occurrence of leopards. In addition, baboons were significantly more likely to be vigilant in areas where intergroup encounters are likely to occur. Finally, baboons were found to be more vigilant on the periphery of their home range.

Table 5.8 Coefficients for variables that influence spatial variation in vigilance patterns (vigilant values as the dependent variable) (Model F; SEM model).

Fixed Effects	**Estimate**	**Std. Error**	**z Value**	**Pr(>|z|)**
Intercept	0.258	0.055	4.680	**<0.001**
Leopard	0.326	0.064	5.086	**<0.001**
Intergroup	0.054	0.016	3.313	**<0.001**
Utilisation Distribution	-0.080	0.032	-2.501	**0.012**

5.4 Discussion

Results from spatial autoregressive models showed that perceived risk was the most important factor to influence range use of baboons within the western Soutpansberg. Such perceived risk was primarily driven by intergroup encounters rather than the probability of encountering leopards, however, such that range use in baboons is driven more by social drivers. These factors outweighed food availability on an annual basis. A seasonal analysis found that although range use throughout both seasons was negatively influenced by intergroup encounters, baboons select areas with high food availability in winter. Interestingly, although vigilance did increase in areas where intergroup encounters are more likely to occur, as well as on the periphery of their home range, results show that predation risk (the probability of encountering a leopard) had the biggest influence on spatial vigilance in baboons. Together, these results show that chacma baboons adapt different behavioural strategies as a response to separate threats that are found throughout the landscape.

The landscape of fear had the biggest effect on space use, with baboons avoiding areas where they are more likely to elicit alarm calls. These results directly contrast those found by both Willems (2007) and Coleman (2013) who found that perceived risk in samango *(Cercopithecus albogularis schwarzi*) and vervet monkeys were primarily driven by the probability of encountering their predators and not by intergroup encounters.

Although baboons do not make predator-specific alarm calls, they do elicit different vocalisations in specific contexts, with female baboons shown to produce alarm calls that range on a continuum. Harsh (towards the end of this continuum and defined as louder and shrill-like) alarm calls were most often elicited under the direct risk from predation, and usually only when the predator was in proximity (Fischer, Hammerschmidt, *et al.*, 2001). In addition, harsher alarm calls (compared to contact calls) were rarely induced under natural conditions. (Fischer, Metz, *et al.*, 2001). Combined, these factors may explain why alarm calls were not only rarely recorded (compared to wahoos), yet also why the probability of a predator encounter did not influence the elicitation of such vocalisations. In contrast, male baboons elicit loud vocalisations described as 'wahoos', which have been hypothesised to have been evolved to be projected from great distances (Fischer *et al.*, 2002). Although wahoos are elicited in response to predators, they are also used far more often during competitive encounters (direct or indirect) between males (Fischer *et al.*, 2002). During long distance communication, wahoos have been shown to relay information regarding not only how far away the call is coming from, yet also the physical condition of the caller (Fischer *et al.*, 2004).

Range use in baboons is primarily driven by avoiding intergroup encounters rather than predation. These results contrast with previous work conducted on range use in primates within the western Soutpansberg. For example, Coleman and Hill (2014) found that perceived risk of aerial predators such as eagles has the biggest influence on space use in semi-arboreal samango monkeys compared to intergroup encounters as well as potential terrestrial predators. In addition, although Willems did not directly assess if between group competition influences space use in the more terrestrial vervet monkeys, he did find that

vervets actively avoided areas that were perceived to be riskier due to baboons or leopards (but not eagles) (Willems and Hill, 2009).

In contrast to predation risk, intergroup avoidance had the strongest effect not only on the probability of eliciting alarm calls, but also space use, with baboons avoiding areas where other groups are more likely to be present regardless of the time of year. The results from my analyses not only complement those found by Markham (*et al.,* 2013), but are also the first to show that spatial avoidance, at least in chacma baboons, also occurs over a longer period than previously recognised. There are several explanations for why chacma baboons exhibit spatial avoidance over long term scales. Unlike samango groups residing in the area, the home range of the focal baboon group overlaps considerably with neighbouring groups in all directions, which therefore may reinforce long term avoidance strategies. In addition, unlike samangos, who primarily reproduce during the dry season, baboons can mate and reproduce throughout the entire year. As aggressive encounters in baboons are more likely to occur when females are in oestrus (Cowlishaw, 1995), it seems probable that the threats imposed by other groups are relatively constant across the year. Given that direct intergroup encounters not only have the potential to escalate into costly and aggressive interactions yet also allow rival males to identify prospective reproductive opportunities (Cowlishaw, 1995; Markham *et al.*, 2013), spatial avoidance may be the most effective as well as least costly strategy to utilise in the long term.

Food availability did not affect space use annually or in summer, yet significantly influenced range use during winter months. The lack of an effect of food availability throughout the entirety of the year as well as summer is most likely due to the overall abundance of food per habitat during such time periods. As such, baboons may not necessarily be driven to allocate their time in specific areas, if most habitats throughout their range contain enough food. In contrast, baboons chose to range in habitats exhibiting a greater abundance of food during winter months. Baboons in the western Soutpansberg must not only face the costs of thermoregulation during cold winter months yet are also constrained to feed for a reduced period (compared to summer) due to limited

daylight hours and food availability. As such, it may be likely that such conditions not only force baboons to forage in patches that exhibit the highest quality food items (despite the risk associated with them), yet also reduce the time it takes to get to such locations by travelling more efficiently (De Raad, 2012).

Baboons did not spatially avoid areas where the probability of encountering leopards increased but instead increased their vigilance while at such locations. It is likely that baboons cannot fully avoid leopards, who are not only present throughout the entirety of their home range, yet also may have to traverse through areas where the probability of encountering such predators are quite high while avoiding other groups or in search of food. Given such circumstances, it may be possible that the only effective anti-predator tactic that can be employed by baboons that does not directly interfere with a reduction in food acquisition is to simply remain vigilant when at such locations.

Such a behavioural strategy has been found in other mammals that must opt to trade off an increase in risk from predators to acquire resources when no other option is given. For example, Valeix (*et al.,* 2009) found several ungulate species to increase their vigilance when in proximity of sparsely located watering holes due to the increased risk of predation from lions. Perhaps one of the most famous examples that assessed spatial variation in vigilance derives from the assessment of elk (*Cervus elaphus*) and bison (*Bison bison)* antipredator strategies after the reintroduction of wolves in Yellowstone National Park (USA) (Laundré, Hernández and Altendorf, 2001). In this instance, female elk and bison were initially found to increase their vigilance levels in areas where wolves were present. Female elk vigilance increased as the years went by and the wolves were able to fully establish themselves on the landscape (Laundré, Hernández and Altendorf, 2001). The authors also found a decrease in foraging effort (20% for female elk with and without calves) due to the trade off between foraging and remaining vigilant while in areas occupied by wolves (Laundré, Hernández and Altendorf, 2001). Such a trade off can potentially lead to not only a reduction in fitness, but a reduced reproductive output, which can

ultimately have population level effects (Laundré, Hernández and Altendorf, 2001). Despite this, baboons (unlike ungulates) may have the ability to scan while foraging and therefore they may necessarily have to trade-off energetic costs in order to remain vigilant through large portions of their home range (Cowlishaw *et al.*, 2004).

Baboon vigilance also increased in areas where the probability of intergroup encounters increased as well as on the periphery of their home range. Unfamiliar areas may be deemed risky since such locations may exhibit a higher risk from potential predators and as such, baboons may act accordingly by increasing vigilance levels. An increase in scanning at home range edges may simply be because baboons may have to put more effort into finding food. Unfamiliar areas have been shown to not only heighten vigilance in primates (Allan and Hill, 2018) yet may also be more dangerous in the event of a direct encounter. For example, Markham (*et al.,* 2012) found that a 'winning' outcome during competitive intergroup encounters in baboons in Amboseli were most likely to be in favour to groups that are more familiar with the area, regardless of how many males are present. That is, successful displacement of another group was likely to occur when one group is more familiar with an area than the other. As such, spatial avoidance may solely reflect a least costly means to prevent direct encounters, yet also alleviate the risks associated with traversing through areas where the probability of losing a direct encounter increases. This is exemplified by the fact that baboons' vigilance also increases where intergroup encounters are likely to occur.

Baboons within the western Soutpansberg Mountains increased their alarm call frequencies and decreased range use in areas where other groups are likely to occur, thus suggesting active avoidance. Although baboons may attempt to avoid areas on the periphery of their home range, complete avoidance may be impossible due to having to share home range boundaries on all sides with different groups. As such, baboons may attempt to minimise the risk associated with direct conflicts with other groups through early detection by increasing their vigilance both on the periphery of their home range as well in areas where such encounters are likely to occur. Similar behaviours have been observed in

other primate species where intergroup encounters have the potential to become aggressive. MacIntosh and Sicotte (2009) found that ursine colobus monkeys (*Colobus vellerosus*) were likely to increase vigilance during intergroup encounters as well in areas where home ranges overlap between two groups. In addition, spider monkeys (*Ateles geoffroyi*) were more likely to increase vigilance on the periphery of their home range, most likely as a means to prevent aggressive interactions between groups (Busia, Schaffner and Aureli, 2016).

This research is the first to utilise localised spatial autoregressive models to assess spatial variation in range use and antipredator behaviour in baboons while not only accounting for the probability of encountering different types of threats (i.e. the probability of encountering other groups and leopards), but also the distribution of resources. Although complex localised spatial autoregressive models are primarily utilised in fields such as spatial econometrics (LeSage and Pace, 2009), the results presented here show that such analyses can (and should) be applied to behavioural-ecological studies that have a spatial component.

Spatial autoregression offers several key advantages over traditional methods (although see Lichstein *et al.*, (2002) for a review on how such methods can be applied to ecological data). Firstly, by accounting for spatial autocorrelation, spatial autoregressive models have the potential to allow for spatial independence between model residuals (Fotheringham, 2009). This is important when considering that data points that are confined to space are also often spatially dependent, and as such, points that are closer to one another will typically have similar values compared to those that are farther away (LeSage, 2008). Accounting for spatial autocorrelation in a spatially explicit model can potentially prevent uncertain or even inaccurate results (Pace and LeSage, 2010).

In addition, spatial regression models can allow researchers to understand how specific underlying explanatory variables influence the geographical patterns of a dependent variable of interest (Anselin, Syabri and Kho, 2006). Observed spatial patterns (such as clustering) can be accurately explained by the

conditions in which they are found (Anselin, Syabri and Kho, 2006). Given the reasons discussed above, as well as the ability to account for localised spillover effects between neighbours (LeSage, 2009), spatial autoregressive models are a powerful tool that can help us understand complex geospatial patterns found in nature.

Finally, this is the only study to date that has used resource selection functions from data derived from leopards to assess long term trends on how primates spatially and behaviourally respond to the *actual* probability of encountering their primary predator (but see Frair *et al.*, (2005); Hebblewhite, Merrill and McDonald, (2005); Hebblewhite and Merrill, (2007) for examples involving ungulates as well as Isbell *et al.*, (2018) for an assessment of short term predation risk in primates). Given the rarity of predation events in primates, it seems likely that such long term behavioural adjustments in response to predation would be difficult to assess with anecdotal observations of predator encounters alone. Resource selection functions provide a valuable method to investigate the environmental factors that influences preferred habitat type (in this case, for leopards) over large scales, which, in turn, predicts where an animal (predator) is likely to occur (Manly *et al.*, 2002) and where a prey item is likely to encounter them (Hebblewhite, Merrill and McDonald, 2005).

These results not only show that perceived risk can dramatically influence range use in baboons, but that such risks are possibly driven by the fear of other groups rather than predation. Finally, and perhaps more importantly, the results from these analyses highlight that baboons engage in different behavioural strategies when faced with risks imposed by both predators and other baboon groups in roughly the same environment. These suggest that spatial avoidance or increased vigilance to prevent conflict can be employed when faced not only with intergroup competition, but also with a threat that is spatially predictable, but which can also be detected with relative ease. In contrast, heightened vigilance alone may be the only antipredator behaviour baboons can afford to use when faced with a predator that not only relies on stealth to attack but is also located throughout the entire home range.

Chapter 6: Illuminating Movement? Nocturnal Activity Patterns in Chacma Baboons (*Papio ursinus*)

Abstract

Recent analyses have shown that typically diurnal primates may occasionally exhibit some levels of activity at night. Despite this, there have been few studies that have explored whether diurnal primates living in temperate environments will extend their activity budgets to the nocturnal phase as a response to seasonal constraints. Using dual-axis accelerometers, I explored whether chacma baboons (*Papio ursinus)* residing in the western Soutpansberg Mountains, South Africa, responded to environmental variables including seasonally fluctuating levels of day length, lunar illumination, wind-speed, precipitation, and temperature, by heightening or lowering nocturnal activity levels. Our results show that chacma baboons engaged in low levels of activity at night throughout the year. Although baboons had heighted nocturnal activity as a response to shorter days, moonlit nights, and lower temperatures, these responses were most likely due to disturbed sleeping patterns rather than more active movement. Nocturnal activity significantly dropped in a female baboon throughout the course of her pregnancy and remained low after giving birth suggesting that females with infants must increase resting. My results complement previous analyses which suggest that although diurnal primates may occasionally be active at night, there is limited evidence for strategic use of the nocturnal phase even in highly seasonal environments.

6.1 Introduction

While most mammals are active at night (nocturnal), several taxa have evolved to be active during daylight hours only (diurnal) or at intermediate light conditions (such as at dawn and dusk: crepuscular), or throughout the 24 hour cycle (cathemeral) (Bennie *et al.*, 2014). Although activity patterns are generally constrained by physiology, morphology, and behaviour, many mammals exhibit remarkable flexibility in switching between nocturnal or diurnal activity patterns in relation to biotic or abiotic cues (Kronfeld-Schor and Dayan, 2003). Factors that have the ability to mask temporal shifts in activity include

competition avoidance (Carothers and Jaksić; 1984), predation (Lima and Dill, 1990), thermoregulation (Chappell and Bartholomew, 1981), and lunar luminosity (Kronfeld-Schor *et al.*, 2013). Since behaviour is generally constrained to the active period, it is essential to understand how extrinsic (environmental) variables enhance or constrain activity budgets and the potential for activity to extend into other phases of the 24-hour cycle.

Animals often react to intensified moonlight by supressing their activity levels (Price, Waser and Bass, 1984; Hecker and Brigham, 1999; Prugh and Golden, 2014) with such lunar-phobic behaviour hypothesised to be an anti-predator defence (Clarke, 1983; Saldaña-Vázquez and Munguía-Rosas, 2013). In contrast, while diurnal mammals typically supress activity at night, there is increasing evidence that some species may exhibit heightened nocturnal behaviour as a response to intensified moonlight (Kronfeld-Schor *et al.*, 2013). Among carnivores, increased activity on moonlit nights has been suggested to aid hunting efficiency (Cozzi, Broekhuis, McNutt, *et al.*, 2012; Rasmussen and MacDonald, 2012; Broekhuis *et al.*, 2014), while among cathemeral primates, increased activity on brighter nights may enhance foraging opportunities and predator detection (Kappeler and Erkert, 2003; Fernández-Duque, de la Iglesia and Erkert, 2010).

Climatic variables including weather patterns such as wind-speed, rain, and temperature have the potential to place thermal constraints on animals by altering their core body temperature (Stelzner and Hausfater, 1986; Hill, 2006; Webster *et al.*, 2008). As a response to harsh climatic conditions, endothermic animals (including primates) will alter their behaviour and activity budgets as an attempt to maintain homeothermy (Hill, 2006; Donati *et al.*, 2011; Majolo *et al.*, 2013; Gestich, Caselli and Setz, 2014). Behavioural plasticity in relation to climatic conditions is perhaps best illustrated in species that live in seasonal environments where fluctuating climatic conditions coupled with limited daylight hours have the potential to alter activity budgets (Dunbar, 1992; Hill *et al.*, 2003; Hill *et al.*, 2004). For example, ungulates and rodents living in environments with high summer temperatures will often switch to foraging at

night as a means to avoid thermal stress (Herman, 1977; Dussault *et al.*, 2004; Bourgoin *et al.*, 2011; Hetem *et al.*, 2012).

In primates, seasonal shifts in activity have been notably recorded in cathemeral species. Mongoose lemurs (*Eulemur mongoz*) living in seasonally dry forests became more diurnal during the wet season when there is lower night time light intensity and yet became chiefly nocturnal during the dry season when day length was shorter (Curtis, Zaramody and Martin, 1999). In less predictable environments that are characteristic of south-eastern Madagascar, brown collared lemurs (*Eulemur collaris*) shifted their activity levels in response to food availability and thus became more diurnally active when ripe fruit was more readily available (Donati *et al.,* 2007). Despite this remarkable seasonal plasticity, there has been no formal investigation to date of whether such flexibility extends to the use of the nocturnal phase in diurnal primates and whether such species can compensate for diurnal time budget constraints, particularly in winter, through nocturnal activity.

Due to practical constraints ranging from inadequate visibility to unintentionally altering natural sleeping habits, previous research on nocturnal activity patterns in diurnal anthropoids has been primarily limited to anecdotal observations (Vessey 1973; Anderson and McGrew 1984; Stelzner and Hausfater 1986; although see Isbell *et al.,* 2017 and Tan *et al.,* 2013). However, recent advances in radio-telemetry have allowed for the collection of activity data through dual axis accelerometers attached to GPS (Global Positioning System) collars. Accelerometers have been especially useful in allowing researchers to monitor the behaviour of cryptic species such as pumas (*Puma concolor*) (Terrie M Williams *et al.*, 2014), badgers (*Meles meles*) (McClune *et al.*, 2014) and lynx (*Lynx lynx)* (Podolski *et al.*, 2013) as well as activity patterns during time periods when behavioural observations are difficult (Cooke *et al.*, 2004; Brown *et al.*, 2013). Accelerometers have also proven effective on primates (including baboons; Markham and Altmann 2008; Fehlmann *et al.* 2017; Isbell *et al.* 2017) and have been employed to assess intragroup (Mann *et al.*, 2005) as well as seasonal variability in activity patterns (Erkert and

Kappeler, 2004; Muñoz-Delgado *et al.*, 2005; Eppley, Ganzhorn and Donati, 2015).

Through the aid of dual axis accelerometers, this research assessed whether temporal, environmental, and physiological factors impact nocturnal activity patterns in chacma baboons (*Papio ursinus*) found in the western Soutpansberg Mountains, Limpopo Province, South Africa. Living in large complex multi-male/multi-female groups, baboons are some of the most widespread primates in Africa (Henzi and Barrett, 2005) inhabiting a variety of different environments that vary significantly in terms of seasonality, food availability, and habitat types (Dunbar, 1992). Chacma baboons respond to environmental pressures including seasonal changes in food availability, temperature, and day length by not only altering their diet, but also by reallocating their time spent engaging in necessary tasks including resting, feeding, and socialising (Dunbar, 1992; Hill *et al.*, 2003)

Despite being considered diurnal, baboons have been recorded shifting activity levels throughout the night as a response to lunar luminosity. For example, yellow baboons (*Papio cynocephalus*) at Amboseli, Kenya, had periods of frequent alarm calling with increased nocturnality (Altmann and Altmann, 1973), whereas Guinea baboons (*Papio papio*) in Sengal were found to regularly move throughout the night and to leave sleeping sites earlier in the morning during the dry season when nocturnal illumination was greater (Anderson and McGrew (1984). Using accelerometers and GPS collars, Isbell and colleagues (2017) found low levels of nocturnal activity in a group of olive baboons (*Papio anubis*) in Laikipia, Kenya, with movement found to occur on 15% of nights, but there was no clear indication that baboons responded to increased moonlight. Although nocturnal activity may be marginal in equatorial baboons, there has yet to be a formal assessment whether populations living in a non-equatorial latitudes exhibit nocturnal behaviour. Such populations are likely to experience significant ecological constraints on time at certain times of year (Hill *et al.*, 2003) such that the adaptive use of the nocturnal phase may allow them to compensate for limits in the diurnal activity period at these times.

Following an assessment that baboons exhibit quantifiable activity levels at night within the Soutpansberg Mountains, South Africa, I then test the following hypotheses:

H1: Baboons will respond to shorter day lengths in winter by extending their activity into the nocturnal phase.

H2: Nocturnal activity will increase on nights exhibiting greater lunar luminosity (i.e. during a full moon) due to increased visual acuity.

H3: Environmental variables will impact nocturnal activity levels due to thermoregulatory constraints. Specifically, activity will decrease as temperature and the wind-chill equivalent temperature decreases and wind-speed increases, and as precipitation increases.

6.2 Methods

6.2.1 Study Site

This study was based at the Lajuma Research Centre in the western Soutpansberg Mountains, Limpopo Province, South Africa (23°06'45.14"S 29°11'37.10"E) between September 2013 and October 2015. The study site has a mean annual rainfall of 724 mm with a summer rainy season (December to February) and a winter dry season (May to August) (Willems, Hill and Willems, 2009). Mean daily minimum and maximum seasonal temperatures throughout the study period ranged from 16.8-17.6°C in winter to 21.2-22.0°C in summer. Mean nightly minimum and maximum temperatures ranged from 12.8-13.4 °C (winter) and 18.6-19.1 °C (summer). Day length fluctuates from approximately eleven hours in winter to over thirteen hours in summer (Section 2.2).

6.2.2 Baboon Collaring Methods and Activity Data Collection

Baboons (N=3) from two groups were fitted with Vectronic GPS-PLUS collars (VECTRONIC, Aerospace, Berlin, Germany) (N=4) between September 2013 and November 2015. one individual was fitted twice over the study period. Collars were programmed to take GPS fixes every hour between 06:00 and 20:00 SAST except for one nocturnal fix at 22:00 (Section 2.4.4). The GPS collars incorporated dual-axis activity sensors which captured acceleration on two axes (X-axis and Y-axis) in two minute intervals. In this case, the X-axis

represents forward and backward movements and the Y-axis sideward and rotary movements (Berger, Dettki and Urbano, 2014). Given the strong positive correlation found between the X-axis and the Y-axis (Pearson's r = 0.953, p= < 0.0001), only the X-axis data were utilised in analysis (following Heurich *et al.,* 2014). Activity values derived from sensors range from 0 (no activity) to 255 (high activity). All GPS collars were designed to fall off 455 days after the collars were fitted, with data downloaded regularly through an Ultra High Frequency (UHF) terminal (Section 2.4.5.)

6.2.3 Predictor Variables

Data from between 20 minutes after the onset and 20 minutes before the conclusion of astronomical twilight were extracted for analysis in order to completely ensure that only nocturnal data were included (Bearder, Nekaris and Curtis, 2006). Astronomical twilight defines a time range when the sun (disc) is 18° below the horizon such that the data selection ensured that baboons could not see without additional illumination. Times for the onset and conclusion of astronomical twilight across the duration to this study derived from the National Aeronautics and Space Administration (NASA) database (http://aa.usno. navy.mil/).

Local climatic data including rain, temperature, wind speed and wind chill equivalent temperature were collected from an on-site SAEON (South African Environmental Observation Network) weather station. The wind chill equivalent temperature combines temperature and wind speed to estimate the perceived environmental temperature (Hill *et al.*, 2004).

Lunar luminosity, defined as the percentage of the lunar sphere that is visible due to illumination by the sun was used to assess whether moonlight influenced baboon nocturnal activity. Lunar luminosity, daily moonrise and set times and day length (being the period in which the Earth receives illumination from the sun) were downloaded from NASA's data services (https://data.nasa.gov/) and synchronized to the dataset. Lunar luminosity was continuous with values ranging between 0% (moon not visible) to 100% (fully visible). Since lunar luminosity is constrained to times in which the moon is visible in the night sky

(above the horizon), lunar luminosity values were limited by moonrise and set times each night.

6.2.4 Statistical Analysis

In order to test the three hypotheses, nocturnal activity data were separated into two different datasets (i) average activity throughout each night within the study period (dataset A) (N=777); or (ii) average activity within a half hour interval (i.e. the average activity within every half hour for each individual night) (dataset B) (N= 14019). The utilisation of two datasets allowed for both a coarse and fine scaled analysis of nocturnal activity. While a broad scale analysis (Model A) allowed for an overall analysis of seasonal trends, a fine scaled model (Model B) permitted the inclusion of environmental variables that may shift throughout the night.

A generalized linear mixed model (GLMM) with a gamma error structure and log link function (Bates *et al.*, 2015) was used to assess total activity levels across nights in RStudio (Version 0.98.1103; RStudio, Inc.). Activity data were transformed by adding a 1 to all values to fulfil the requirements for a gamma GLMM.

Day length was included in both coarse and fine-grained models to address whether baboons responded to shorter days by extending their nocturnal activity levels throughout the night (H1). To assess the impact that the lunar cycle had on baboon activity levels (H2), lunar luminosity was included in the coarse grained model (Model A), with the luminescence value corrected for the presence of the moon combined in Model B (fine grained model). Mean nightly wind chill temperatures and precipitation levels were included in Model A to assess the impact of weather variables (H3). Temperature, wind speed (and the interaction between the two), and precipitation levels at half hour intervals were included to assess whether fluctuating environmental variables had a fine-grained influence on baboon nocturnal activity levels.

To account for intergroup, individual, and nightly variability, collar identity (N=4) specific groups (N=2), night (N=777), sleeping site identity (derived from the nocturnal GPS fix and ground-truthed with observational data, N=19) were

included as random effects. One collared female gave birth during data collection. The presence of an infant was thus included as a factor to account for the costs of maternal care such as infant carrying, suckling and increased vigilance (Altmann and Samuels, 1992; Rendall, Cheney and Seyfarth, 2000; Maestripieri, 2011) impacting on nocturnal activity. Subsequent results were analysed in RStudio and visualised with the aid of the ggplot2 package (Wickham, 2009).

6.3 Results

Although nocturnal activity levels were below those observed during the day (Diurnal, N = 777, $\bar{x}$= 64.57, SE= 0.379; Nocturnal, N=777, $\bar{x}$= 1.76, SE = 0.029), consistent, but low levels of activity were observed during the nocturnal phase, with more intermediate levels of activity in the twilight phases (Figure 6.1).

Model A included lunar luminosity, wind-chill equivalent temperature, precipitation and day length as predictor variables (Table 6.1) and represented a significant improvement over the null model (the control variables, presence of an infant, day length, and random effects (likelihood ratio test: x^2 = 80.42, df = 4, p= < 0.0001). In support of hypothesis 1, a significant negative relationship between day length and nocturnal activity levels suggests that baboons increase nocturnal activity as day length declines. In support of hypothesis 2 there was a significant positive relationship between baboon activity levels and lunar luminosity with baboons more active on nights exhibiting greater light intensity. There was no support for hypothesis 3 that lower perceived temperature (through wind chill) as well as higher levels of nightly precipitation impacted baboon activity patterns throughout the night. Nocturnal activity significantly decreased with the presence of a dependent infant.

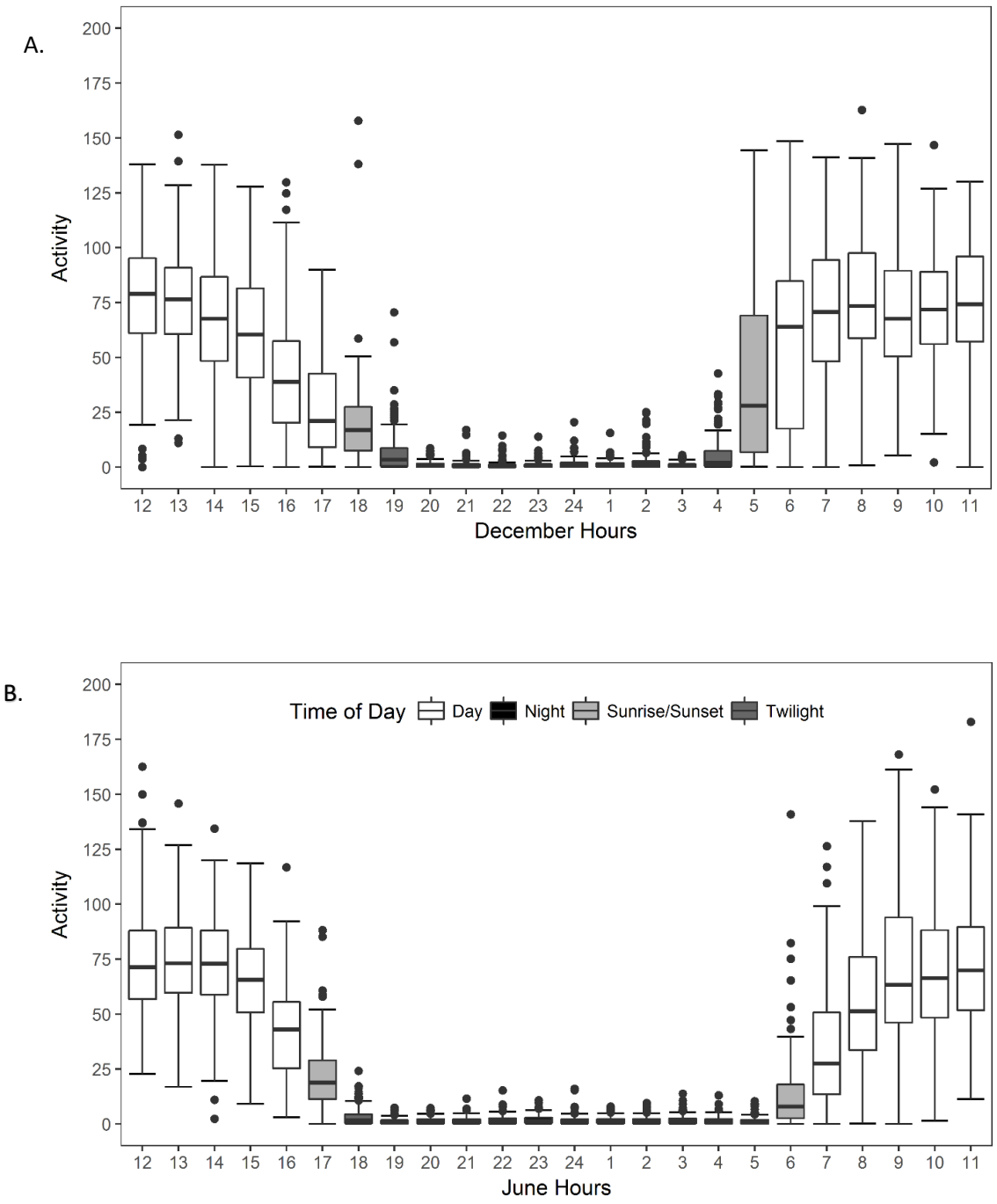

Figure 6.1 Boxplots (median, lower and upper quartiles, and one standard error) of activity levels across the 24-hr cycle under conditions of A) maximum day length/minimum night length in summer (December; mean day length: 13h 31m). Activity levels range from 0 (low activity) to a maximum of 255 (high activity). B) minimum day length/maximum night length in winter (June; mean day length: 10h 44m).

Table 6.1 Coefficients for coarse grained analysis from gamma error GLMM of seasonal nocturnal activity (dependent variable is average activity values across the night) random effects include individual, night, sleeping site, and baboon group).

Fixed Effects	Estimate	Std. Error	t value	Pr(>|z|)
(Intercept)	2.0286	0.1665	12.179	**< 0.0001**
Lunar luminosity	0.0741	0.0259	2.859	**0.0042**
Wind chill	-0.0010	0.0024	-0.421	0.6734
Precipitation	0.0526	0.0407	1.292	0.1964
Day length	-2.2643	0.3176	-7.129	**< 0.0001**
Infant presence	-0.3312	0.0399	-8.288	**< 0.0001**

Model B assessed a fine scale analysis of activity throughout the night and included combined moon presence and lunar luminosity, and temperature and wind speed and their interaction (Table 6.2). Overall, the full model was highly significant compared to the null model (including random effects, day length, and presence of an infant) (x^2 = 17.52, df = 5, p= 0.003). In support of hypothesis 2, lunar light intensity had a significant positive effect on baboon nocturnal activity levels, with activity increasing with higher nocturnal illumination. There was no support for wind speed or precipitation impacting nocturnal activity levels, nor the interaction between temperature and wind-speed. In contrast to expectations, there was a significant negative relationship between temperature and activity levels, with activity increasing when night time temperatures were coldest**.** The reduction in activity levels in the presence of an infant remained significant, as was the relationship with day length.

Table 6.2 Coefficients for fine grained analysis from gamma error GLMM of trends in activity throughout the night (dependent variables being nightly activity level values averaged in half hour intervals; random effects include individual, night, sleeping site, and baboon group).

Fixed Effects	Estimate	Std. Error	t value	Pr(>|z|)
(Intercept)	2.3390	0.1662	14.071	**< 0.0001**
Lunar luminosity	0.0483	0.0210	2.297	**0. 0216**
Temperature	-0.0079	0.0029	-2.661	**0.0077**
Wind-speed	-0.0042	0.0050	-0.843	0.3992
Precipitation	-0.0084	0.0163	-0.516	0.6061
Temperature:wind speed interaction	0.0005	0.0003	1.574	0.1154
Day length	-2.4552	0.3468	-7.079	**< 0.0001**
Infant presence	-0.3021	0.0369	-8.168	**< 0.0001**

6.4 Discussion

A coarse grained model (Model A) indicated varying levels of daylight hours and lunar light intensity may alter activity patterns in baboons residing in the western Soutpansberg Mountains. Subsequently, a fine scale analysis demonstrated that temperature, the presence of the moon (coupled with lunar light intensity), as well as day length impacted baboon activity levels throughout the course of the night, in support of all three hypotheses. For both analyses, the presence of an infant had a significant negative effect on the nocturnal activity levels of the adult female. Although baboons show low, yet consistent levels of nocturnal activity throughout the year, it seems possible, that such patterns may reflect minimal sleep disturbances rather than specific behaviours.

In support of hypothesis 1, baboons increased their nocturnal activity levels in response to shorter day lengths in winter. As previous studies have described the importance of day length in constraining the activity budgets of diurnal primates living in seasonal environments (Hill *et al.*, 2003; Ménard *et al.*, 2013), it is possible that baboons may engage in social activities that may otherwise be severely constrained by shorter day lengths and increased diurnal foraging in winter. However, given the low nocturnal activity in general it is far more likely such an increase may possibly be due to longer nights during winter exceeding

the time needed for sleep. As such, although baboons exhibited higher activity levels during these periods, they more likely reflect that the animals are awake and shifting position slightly rather than more active activity bouts after dark.

Lunar luminosity had a positive effect on nocturnal activity levels in both models, supporting hypothesis 2. Baboons were more active on nights exhibiting greater lunar light intensity, but only at times when the moon was visible above the horizon. Baboons did not travel or forage with increased lunar luminosity and remained on their relatively narrow sleeping cliffs at night. Although baboons in the western Soutpansberg Mountains have been recorded being predated on by leopards on their sleeping sites at night, it seems possible that lunar luminosity may inhibit leopards from attacking. This is primarily because ambush predators (such as felids) are generally less successful at hunting at such times due a reduction in ambush cover that would otherwise be provided on darker nights (Sunquist and Sunquist, 1989).

While many nocturnal and cathemeral primates exhibit higher activity levels on full moons (Gursky, 2003; Kronfeld-Schor *et al.*, 2013) it seems likely that for many species, nights exhibiting greater light intensity may simply have a stimulating effect that supersedes standard circadian activity patterns (i.e. positive masking) (Donati *et al.*, 2013). Such an effect may be especially true in primate species such as chacma baboons that lack a specialised visual structure that aids in nocturnal vision (*tapetum lucidum*). Although baboons in western Soutpansberg exhibited greater nocturnal activity patterns compared to those in equatorial Amboseli (Isbell *et al.*, 2017), there is still no evidence for any significant movement This is reflected in the average distance moved between 20:00 and 00:00 as captured by GPS collars (avg: 35.86 m, N=623). As such, an increase in nocturnal activity with increased moonlight possibly reflects disturbed sleep patterns resulting from the increased nocturnal luminosity.

Female baboons in the western Soutpansberg increased their activity on nights with cooler temperatures, which supports hypothesis 3. Baboons, like other primates and mammals, are known to respond to thermoregulatory constraints by huddling with one another (Gilbert *et al.*, 2010).While such a strategy allows for heat conservation, previous research on Guinea baboons suggests that

individuals may often alter their positions throughout the night as a response to changing climatic conditions (such as wind speed and rain) (Anderson and McGrew 1984). The significant effect of temperature on baboon activity in the western Soutpansberg may possibly reflect localised conditions and sleeping site preference and a response to colder conditions by changing huddling positions throughout the night. Although Anderson and McGrew (1984) did not find temperature to have an effect on postural adjustments, it should be noted that the relatively warmer conditions that are characteristic of Niokolo Koba National Park, Senegal may negate the need for such behaviours.

An interesting outcome of the analysis was that nocturnal activity levels for one female dropped significantly after giving birth (Figure 6.2). While this might be in contrast to predictions that infant presence may increase activity, it should be noted that with the exception of one non-human primate study (Fite *et al.*, 2003), such expectations were driven primarily from research involving maternal sleep disturbances in human mothers (Nishihara and Horiuchi, 1998; Dennis and Ross, 2005; Goyal, Gay and Lee, 2007). In the context of baboons, there have been several studies highlighting the costly demands associated with infant rearing (Dunbar and Dunbar, 1988; Altmann and Samuels, 1992). Interestingly, Barrett and colleagues (2006) found that baboons at De Hoop did not increase time spent feeding as a response to infant rearing but instead suppressed their diurnal activity levels by resting more frequently during the day (possibly due to general fatigue after giving birth). The results here suggest that females with infants may also increase resting and inactivity at night. It should be noted, however, that the activity sensors utilised in this study were not able to pick up subtle behaviours associated with infant suckling. Nevertheless, the fact that nocturnal activity also declines across pregnancy (Figure 6.2) suggests that there are energetic consequences of pregnancy and infant rearing that are reflected in increased resting requirements at night.

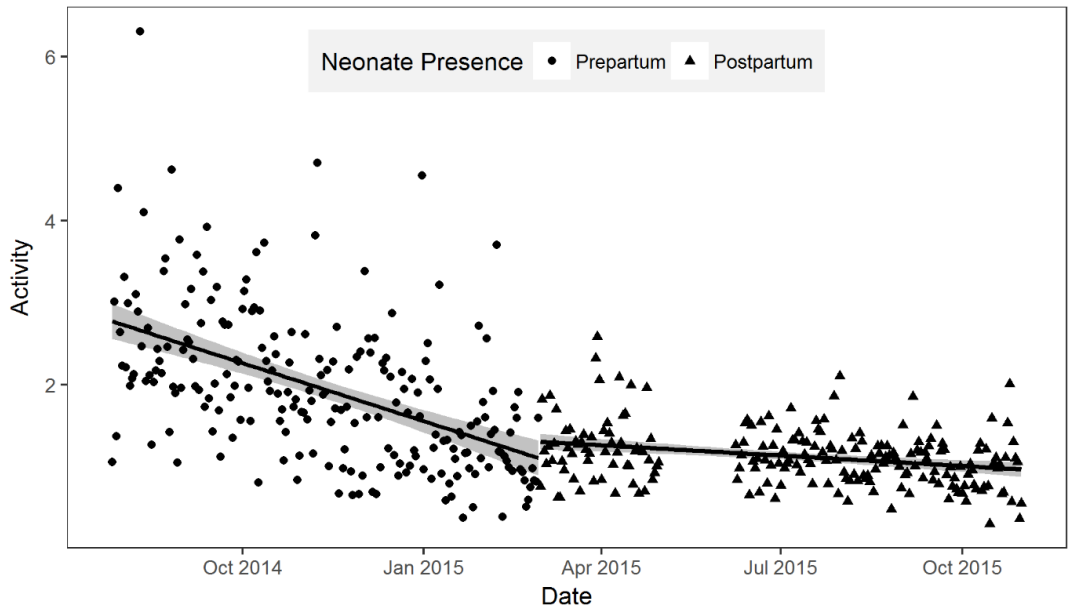

Figure 6.2 Relationship between nightly nocturnal activity levels and the presence of an infant (one activity value per night).

Despite having been effective in the assessment of primate movement (Papailiou, Sullivan and Cameron, 2008; McFarland *et al.*, 2013), the data derived from accelerometers in this analysis can only be utilised to assess how overall trends in nocturnal activity are impacted by a specific attribute. Since the GPS collars attached to the focal baboons only collected a single fix at night it was not possible to supplement this information with additional behavioural data. While the rise in nocturnal activity after shorter days and on moonlit nights probably points to baboons making small adjustments, additional date are needed to assess whether baboons reallocate specific behaviours to the nocturnal period. Infrared cameras have successfully been utilised to assess nocturnal behaviours in diurnal species (Barrett *et al.*, 2004; Gula *et al.*, 2010; Thuppil and Coss, 2015) and may therefore be valuable for remotely determining temporal trends in nocturnal activity. In addition, fine-scale GPS data in conjunction with accelerometers should also permite more refined analysis (Fehlmann *et al.*, 2017).

Baboons exhibit a consistent, yet very low increase in nocturnal activity when days are shorter, lunar luminosity is greater, and when temperatures are lower. Given that the effect sizes of the relationships are modest, it seems likely that sleep is simply more interrupted under conditions of long winter nights, high

lunar illumination and at cold temperatures. Future research should thus focus on identifying the precise behaviours exhibit during heightened activity during the nocturnal phase to better understand how diurnal primates living in temperature latitudes respond to fluctuating environmental conditions.

Chapter 7: Discussion

7.1 Introduction

Predator-prey interactions are a fundamental component of the behavioural ecology for most living taxa. In particular, the risk of predation has been hypothesised to be an important selective force regarding the physical and behavioural evolution found in primates (Isbell, 1994). To minimise the risk of predation, primates have been found to adopt a range of behavioural modifications including group living (Hill and Lee, 1998), spatial avoidance (Willems and Hill, 2009; Coleman and Hill, 2014), alarm calls (Zuberbühler, Jenny and Bshary, 1999; Arnold, Pohlner and Zuberbühler, 2008; Cowlishaw, 2010; Isbell and Bidner, 2016), and vigilance (Campos and Fedigan, 2014; Busia, Schaffner and Aureli, 2016). In addition, primates may also have to spatially and temporally modify their behaviour due to other challenges such as seasonality, food availability, and intergroup conflict while simultaneously avoiding the risk from predation. Although the behavioural responses under the face of predation have been well documented in a range of primate species (Ramakrishnan and Coss, 2001; Willems and Hill, 2009; Coleman, 2013; Bidner, 2014; Campos and Fedigan, 2014), there have surprisingly few studies that have incorporated behavioural data deriving from carnivores on site while assessing long term antipredator responses. This is also despite the suggestions made by Isbell (1994) who recommends that the incorporation of predator studies are fundamental towards understanding predator-primate interactions.

This is startling considering the fact that most predators are not uniformly distributed on the landscape, and they must also make behavioural decisions regarding where to reside and forage as well as when to be active as means to enhance their own fitness (Hebblewhite, Merrill and Mcdonald, 2005; Balme, Hunter and Slotow, 2007; Davidson *et al.*, 2012; Dellinger *et al.*, 2013). As such, in order to attain a comprehensive understanding of predator-prey interactions between two different species residing in the same system, one should ideally also invest in the understanding of the behavioural ecology of the predator as a

means to also understand the antipredator and spatial responses induced by prey.

My primary aims for this thesis were to independently examine long term trends in space use and activity patterns in both chacma baboons (*Papio ursinus*) and their primary predator, the leopard (*Panthera pardus*), as a means to understand how their behavioural ecology is influenced by factors including habitat characteristics, seasonality, and perceived risk. With this knowledge, I then ultimately aimed to assess the spatial variability in perceived risk in baboons in response to my understanding of the specific behavioural characteristics derived from leopards residing at the same study site.

7.2 Summary of Findings

In chapter 3, with the aid of GPS collars deployed on leopards (N=8), I assessed resource selection functions (RSFs) at three different spatial scales throughout the mountain range. I measured how specific environmental factors influenced where leopards are likely to establish home ranges throughout the western Soutpansberg Mountains (2nd order), how such factors influence where leopards are likely to occur within their home range (3rd order) and finally, where leopards are more likely to consume their prey (4th order).

Results from 2nd order RSFs showed that leopards are likely to establish home ranges in elevated, sloped areas that are characteristic of the mountain range. In addition, leopards selected areas that had increased surface ruggedness as well as high vegetation productivity (NDVI). Combined, these results complement previous research which suggests that habitat suitability in leopards is positively influenced by the presence of both rugged and heavily vegetated areas which may not only contain an abundance of prey, yet also sufficient areas to hunt (Edgaonkar, 2008; Gavashelishvili and Lukarevskiy, 2008; Pitman *et al.*, 2013; Fattebert *et al.*, 2015). Similar to large felid populations, leopards in the western Soutpansberg chose to establish home ranges at greater distances from human settlements, thus suggesting active avoidance (Ngoprasert, Lynam and Gale, 2007; Zarco-González *et al.*, 2009; Zeller *et al.*, 2017).

In addition, results from 3rd order RSFs suggested that leopards are more likely to occur in areas within their home range that are heavily vegetated. It seems likely that leopards prefer to utilise highly vegetated areas due to the abundance of preferred prey (particularly small to medium sized ungulates) as well as the fact that such areas likely aid in hunting by providing sufficient ambush coverage. Additionally, leopards were likely to avoid areas within their home range that were in proximity to human settlements.

Remarkably, leopards hunted uniformly throughout their home range (4th order). Although seemingly contradictory given the fact that leopards, like other felids, rely on specific habitat characteristics in order to successfully subdue prey (Sunquist and Sunquist, 1989), it is also possible that the most preferable areas within their home range (i.e. rugged areas exhibiting high vegetation productivity) already provide both a sufficient abundance of prey as well as adequate stalking conditions.

In chapter 4, I assessed how leopard activity levels altered spatially as well as temporally with the aid of dual-axis accelerometers within the GPS collars. I also assessed if leopards that went off the mountains, and into anthropogenic habitats (i.e. agricultural areas) were likely to shift their activity levels in response to an increase in the presence of humans.

Temporally, leopards within the western Soutpansberg Mountains are likely to exhibit crepuscular activity patterns and, as such, are more likely to become more active during twilight hours in the morning and evening than during the day or night. These activity patterns were exhibited year round, suggesting that leopards respond to the seasonal variability in sunrise and sunset times by shifting their activity to coincide with such periods. While all leopards were more likely to be active during twilight hours, there was some variation between the sexes with females being more active during the day. Leopard activity patterns were also influenced by weather conditions; they were found to decrease their activity under warmer temperatures and increase their activity patterns during periods exhibiting heavier precipitation and stronger winds. The increase in activity during heavy rain and strong winds may be due to enhanced hunting conditions, as such weather patterns can potentially mask

the ability for prey items to detect ambush predators (Muñoz, Kapfer and Olfenbuttel, 2014; Cherry and Barton, 2017).

Spatially, leopards were found to decrease their activity at greater distances away from human settlements as well as in sloped and heavily vegetated areas. As the results from the resource selection functions show that leopards also prefer to reside in such areas, it seems likely that such a decrease in activity may be due to such areas acting as refuges. As forested and sloped areas may be ideal to hunt in, it may be possible that such lower activity levels reflect the hunting mode utilised by leopards, who must often remain still while waiting to ambush prey.

Interestingly, leopards were more active in low lying areas outside of the mountains and into human dominated areas. In addition, leopards were also found to shift their activity patterns when in anthropogenic habitats by decreasing diurnal activity and increasing nocturnal activity. As land owners have been found to persecute leopards on their property due to the perceived risk that such carnivores may impose on livestock (Chase Grey, Bell and Hill, 2017) , it seems likely that behavioural adjustments found in my analysis show that although anthropogenic habitats may have a sufficient amount of prey, leopards may possibly be aware of the risk imposed when venturing into such locations.

In chapter 5, I examined whether space use in baboons was negatively influenced by areas that they perceived to be riskier (through the probability of eliciting vocalisations). In addition, as baboons do not give threat-specific alarm calls, I also examined whether such vocalisations were related to the probability of encountering leopards or other groups. Following this, I assessed the influence predation risk, intergroup encounters, and food availability had on both annual and seasonal space use patterns Finally, I assessed whether vigilance varied spatially on the periphery of their home range as well as in relation to the risk imposed by leopards and intergroup encounters.

Baboon space use was negatively influenced by the probability of eliciting alarm calls, thus suggesting that they spatially avoid areas that they perceived to be

riskier. However, this landscape of fear in baboons was only related to intergroup encounters, and as such, baboons were more likely to vocalise when in areas where the probability of intergroup encounters was high. In addition, a subsequent analysis found that annual space use in baboons was also related to intergroup encounters and not to predation nor food availability. Seasonal space use showed similar trends with the exception of winter months, when range use was positively influenced by food availability, suggesting that baboons will possibly trade off safety for greater foraging opportunities when food availability is limited.

Finally, the probability of encountering leopards had the greatest effect on the spatial variation in vigilance patterns in female baboons. Vigilance levels also increased on the periphery of their home range, as well in areas where the probability of intergroup encounters increased. Combined, these analyses suggest that baboons may adapt different behavioural strategies when faced with different threats. Spatial avoidance may act as a long term strategy in males as a means to reduce the reproductive success of potential rivals. In contrast, an increase in vigilance may be particularly useful in response to the risk of predation from a predator that primarily relies on stealth to successfully subdue prey.

In chapter 6, I assessed whether female chacma baboons (who are primarily diurnal) exhibited periods of nocturnal activity in response to abiotic conditions such as seasonal changes in daylength, weather conditions (temperature, wind speed, and rain), as well as moonlight. While overall, baboons exhibited low levels of nocturnal activity throughout the year, they were likely to increase their activity during winter, when daylight hours decreased. In addition, baboons also increased their nocturnal activity on nights exhibiting greater lunar luminosity, and decreased activity on cooler nights. In addition to abiotic factors, I also found that a female baboon's activity level dropped significantly in the months after giving birth. The minimal activity patterns found here suggest that variables such as moonlight may simply disturb sleep patterns rather than promote specific behaviours (such as grooming) after dark.

7.3 Implications of my Findings

To my knowledge, the content in this thesis represents one of the few studies that has utilised a combination of long term spatial, activity, and behavioural data to assess the behavioural ecology of a predator, and its prey (independently) in the same habitat. In addition, this is one of the few studies that has utilised important environmental (such as food availability, water, refuges) and intraspecific competitor data, as well as site specific information directly deriving from the predator to assess long term patterns in space use and perceived risk within a prey species. The results from these analyses show that the behavioural patterns in space and activity use are inherently complex in both species and as such, are driven by a combination of resource acquisition and risk avoidance. In addition, my findings give further support that one should ideally understand both trophic actors to study the predator-prey interactions between them.

7.3.1 The Landscape of Fear: And the Importance of Bringing Back Predators to Predator-Prey Studies.

How carnivores modify their activity and spatial behaviour in response to biotic and abiotic conditions allows for a greater understanding of how they respond to environmental conditions, as well as where and when prey items are more likely to be at risk. Although spatial variation in perceived risk (through alarm calls or increased vigilance) has been assessed in primates before (Willems and Hill, 2009; Coleman and Hill, 2014), there have been very few studies which have used data deriving from the predators themselves in order to assess if such antipredator strategies are a direct reflection on the probability of being attacked. In addition, many studies have assessed the effects that predators have on primates through experimental work (i.e. using model predators (Coss, Ramakrishnan and Schank, 2005; Arnold, Pohlner and Zuberbühler, 2008) or audio recordings (Friant, Campbell and Snowdon, 2008)) or directly, through the rare opportunity when a researcher is able to observe predation attempts, and the behavioural modifications following. In addition, previous studies on primates that have incorporated "the landscape of fear", that is, how primates behaviourally and spatially modify themselves on the landscape due to

perceived predation, have often relied on the location of alarm calls (some of which are predator specific (Willems and Hill, 2009; Coleman and Hill, 2014). While useful, all of these studies neglect one major component regarding predator-prey interactions: the behavioural ecology of the predator!

In addition to the threat posed by predation, many primate species may also occasionally be at risk from encountering other groups within conspecifics, and such encounters have the ability to escalate to violence (Shopland, 1982; Wilson, Wallauer and Pusey, 2004). Knowing where such threats such as predators and other groups are more like likely to occur on the landscape allows for a greater understanding of the actual effectiveness of antipredator strategies (Lima, 2002), and also if the prey use different behavioural strategies that vary depending on the specific type of threat.

The results of my analysis show that baboons in western Soutpansberg not only increase vigilance and vocalisations in areas where encounters with other groups are likely to occur, but also adopt long term spatial avoidance strategies to prevent such encounters from occurring. In contrast, as baboons may not be able to avoid leopards throughout the landscape, they choose instead to greatly enhance their vigilance levels when in areas where leopards are likely to occur. The results from these studies are important for several different reasons.

Firstly, although prey do not always know where their predators are located in their environment, it seems plausible that the baboons studied here, may to some extent, understand the areas in their home range that are potentially dangerous and adjust their behaviour accordingly through increased vigilance or direct avoidance. Although it is highly likely that baboons have a greater understanding of where other groups are likely to occur due to both range overlap and direct cues (such as visual or auditory signalling), the increased vigilance found in areas where the probability of encountering leopards is high also suggests that they possibly have the cognitive ability to spatially recall areas on the landscape that are potentially dangerous from predators and, developed long term strategies to prevent such attacks from occurring. As such, these findings not only show that an increase in scanning may potentially reflect actual risk (rather than perceived risk) when faced with an ambush predator,

but also that baboons exhibit long term spatial memory that allows them to adjust their behaviours in such areas.

Before assessing whether baboons responded to leopard resource selection functions, I tested whether diurnal leopard activity levels influenced their spatial patterns in range use, vigilance, and perceived risk (Appendix 3; Figure S3.1). Diurnal patterns in leopard activity had no effect on the spatial variation found in vigilance, perceived risk, or spatial avoidance of the baboons. There are several explanations for why baboons might respond to the probability of encountering a leopard on the landscape compared to where leopards are more likely to be active. For one, the lack of an effect could simply be because where a leopard is active is of little importance to baboons (and ultimately unknowable) outside of an immediate encounter. This is particularly likely given both the hunting style of the predator, as well as the study system. For example, as ambush (and cryptic) predators that prefer to range in dense habitats (Sunquist and Sunquist, 1989), leopards most likely do not exhibit heightened activity in front of baboons outside of a direct attack. Another possibility may also simply be because leopards primarily exhibited lower activity levels during daylight hours in areas where they also prefer to reside (and are likely to be encountered) (Chapter 4). As such, the lack of an effect may also be due to such low activity values being attributed to where leopards are likely to occur. However, as I also found that leopards increased their activity under weather conditions such as strong winds and heavy precipitation (which may also aid in hunting), I predict that it is possible for baboons to be more at risk under such conditions during the day. Future research on predator-prey interactions should therefore assess if risk may fluctuate under different weather patterns.

The ability to recall where predators are likely to occur, and as such, respond accordingly may have been particularly useful as a terrestrial primate species evolved and radiated throughout the Plio-Pleistocene in habitats that contained a greater array of ambush predators (such as sabretooth cats and false sabre tooth cats) than found throughout Sub-Saharan Africa today (Arribas, 1999). In addition, spatial memory pertaining to the probability of encountering predators may have also been found in early hominins, who not only evolved

under similar conditions as baboons (Codron *et al.*, 2008), yet may have eventually extended such an adaptation from vigilance or spatial avoidance, to also include food acquisition through the scavenging of carnivore kills.

An additional important finding from my analysis is that baboons adopt different strategies when faced with different types of threats. For example, they will use an array of strategies ranging from spatial avoidance to increased vigilance when faced with competition from other groups that has the potential to escalate into aggression and may also induce reproductive constraints. In contrast, vigilance seems to be used when faced with a predator that not only depends on ambush to subdue prey but is also present throughout their home range. These different strategies suggest that baboons are not only more behaviourally complex than previously thought yet must also trade off specific fitness enhancing opportunities when faced with different threats. For example, although baboons increase their vigilance levels when in areas where leopards are more likely to occur, they must still balance risk with food acquisition in such areas. In contrast, baboons seem to exhibit several behaviours, including active avoidance when faced with competition with other groups. While avoidance may limit the reproductive success of rival males while simultaneously preventing potentially dangerous interactions, such strategies might also have negative consequences. For example, such long term avoidance strategies may not only prevent baboons from accessing potentially important sources (sleeping sites, food patches), but may simultaneously force them to feed in areas that are riskier due to the presence of leopards. In addition, the long term perceived risk induced by other groups may potentially lead to both energetic and physiological consequences which in itself can influence reproduction output, survival, and ultimately population dynamics.

Finally, the combined results presented by myself, as well as Coleman and Hill (2014) and Willems and Hill (2009) represent some of the only studies to assess the influence that perceived risk and resource distribution has on space use in different primate species (vervet, (*Chlorocebus pygerythrus*), samango (*Cercopithecus albogularis schwarzi*), chacma baboon) at the same study site. Results from these analyses suggest that despite inhabiting a similar area, the

factors that affect space use in these primate species vary considerably and are possibly influenced by body size, terrestriality (or arboreality), and behaviour. For example, perceived risk through spatial avoidance in chacma baboons seems to primarily be explained by intergroup encounters rather than direct predation. These results contrast those found by Coleman and Hill (2014) who found that intergroup encounters had little effect on space use compared to the risk imposed by arboreal predators. In addition, primates exhibiting a more terrestrial lifestyle were more likely to respond to terrestrial threats such as leopards (avoidance in vervets, vigilance in leopards) as well as other primates (primarily other baboons). Even then, vervets and baboons exhibit some different (as well as same) antipredator strategies when faced with threats such as leopards or baboons. In this case, baboons opt to utilise vigilance (compared to spatial avoidance) when faced with leopards, whereas both vervet monkeys and baboons spatially avoid baboons. It seems likely that the difference in response to threats such as predation is likely to be due to the different levels of pressure imposed on these species. While all three species may be technically at risk from predation by leopards, it seems likely that vervet monkeys are predated on more frequently due to their small body size and terrestrial lifestyle. This is complemented by the fact that previous analyses on leopard diet within the Soutpansberg found that vervet monkeys accounted for 12.2% of the relative frequency of prey being consumed compared to baboons (4.3%) and samango monkeys (2.1%) (Chase Grey, Bell and Hill, 2017). In addition, the lack of an effect that intergroup encounters had on samango monkeys (compared to baboons) may be explained by the fact that out of all three diurnal primates within western Soutpansberg-, baboons are the only species to be directly surrounded by other groups. As such, direct encounters are not only more likely, but baboons may additionally have to adopt a range of strategies including long term avoidance to alleviate any potential conflict. Combined, these results highlight how primate species residing within the same geographical area not only face different types of threats, but also respond in various ways providing valuable insight regarding the behavioural ecology of primate species.

7.4 Limitations of the Study

There were several limitations to my study that must be noted. For one, although it is likely that 4th order resource selection in leopards are uniform throughout their home range due to the sufficient amount of prey as well as areas to ambush, it should be noted that I was unable to directly confirm the locations of all kills. As such, it is possible that 4th order resource selection functions found here may not be as accurate as the previous scales (2nd and 3rd order). The inability to confirm kill sites was partially due to financial and time constraints that prevented me from spending an adequate amount of time searching for kills in western Soutpansberg. In addition, I discovered through personal experience that many kills did not remain on the landscape by the time I began this study. This is most likely because many were not only relatively old (2-3 years old), but also due to the presence of brown hyenas (*Hyaena brunnea*) who actively scavenge kills and consume bone (Owens and Owens, 1978).

An additional limitation that should also be noted is that the leopard GPS data utilised to create resource selection functions did not fully temporally overlap with the baboons data (leopard data stopped recording in July 2014). Therefore, the probability of occurrence for leopards within their home range can technically only apply to the years 2012 and 2014 (and not 2014-2017). As such, it would have been ideal to have utilised leopard resource selection functions that temporally overlapped with the time periods that baboon spatial and behavioural data were collected. Despite this, it should also be noted that the increase in vigilance found in the baboons in response to the probability of encountering leopards combined with the continuous trend for leopards to utilise areas exhibiting heavily vegetation suggests that home range utilisation in leopards changed little over the study years.

This concern over the lack of temporal overlap between data from the two species can also be extended to seasonal space use in baboons. Seasonal resource selection functions in leopards were not assessed and as such, I do not know if home range use in leopards varied between summer and winter. Seasonal space use in leopards has been known to vary, with some populations shifting their space use in response to the seasonal distribution of prey

(Grassman, 1999; Odden and Wegge, 2005), and others remaining relatively stationary throughout the year (Marker and Dickman, 2005; Fattebert *et al.*, 2016). It is therefore possible that the lack of an effect for spatial avoidance in baboons due to perceived risk from predators during summer and winter may be because leopard RSF do values not accurately reflect risk from these predators during the same time periods. Future studies that aim to incorporate the effect predation has on seasonal space use in prey should also thoroughly investigate whether seasonality influences habitat use in predators.

Although the focal baboons spatially avoid areas where the probability of intergroup encounters increased as well as increased their vigilance in such areas, as well as on the periphery of their home range, I unfortunately had very little spatial data directly deriving from the other baboon groups. Such data would have been useful for a variety of reasons. For one, it would allow me to assess if focal baboons directly avoided the home ranges for other groups outside of the contexts of the probability of direct encounters as utilised in my study. Additionally, it would allow me to assess if different groups residing in the area exhibit similar (or different) patterns of space use in response to food availability as well as perceived risk both from other groups and predation. Such findings would be particularly interesting given the fact that predation risk and food availability in particular, most likely varies throughout the western Soutpansberg.

An additional limitation that could not be prevented is the fact that the focal baboons are habituated. Although there is evidence that behaviour (including ranging behaviour) may not be heavily influenced by the presence of a human observer (Crofoot *et al.*, 2010), there is also evidence suggesting that humans may have the potential to influence perceived risk (Nowak *et al.*, 2014), and predation rates (Isbell and Young, 1993), as well as the outcome between intergroup encounters (Zinner, Hindahl and Kaumanns, 2001). Although the focal baboon group are occasionally predated on, it may be possible that predation rates are actually lower compared to other groups due to the presence of a human observer. As such, this may partially explain why both spatial avoidance and alarm calls were not attributed to the probability of

encountering leopards. In addition, although baboons were found to respond to other groups through an increase in alarm calls, spatial avoidance, and heightened vigilance, it may be possible that direct encounters occurred less than they would have without the presence of an observer. Given these possibilities, it seems likely that assessing the perceived risk for both a habituated and unhabituated group would address these issues.

Although accelerometers were useful in assessing activity levels in baboons at night, it seems likely that such an analysis could be improved with the use of spatial data at such time periods. Unlike the leopard GPS collars, baboon fixes were taken predominately between sunrise and sunset with the exception of one nocturnal fix that occurred at night. As such, it was impossible to assess if the baboons engaged in physical movements such as walking during such time periods. In addition, as most predation events during the study period happened at night or in the early morning, the incorporation of GPS collars that continuously recorded nocturnal activity may allow for an assessment of nocturnal risk. Such data may improve our understanding of not only sleeping site selection, but also whether range use is, in part, influenced by the events that occur at night. In addition, it would have been ideal to have been able to assess whether the increase in activity levels during winter months was due to the baboons having to maintain social bonds through activities such as grooming during time periods exhibiting limited day length. Although accelerometers can pick up broad levels of activity, it should be noted that it is possible that they are unable to record stationary behaviours such as grooming. As such, it is highly recommended that future research that aims to assess nocturnal activity in a diurnal species should incorporate not only accelerometers, but also video cameras, which would allow researchers to determine the exact behaviours conducted at night.

Future Research

The content in this thesis addressed my primary aims and objectives and the results found have the potential to give way to future research on not only predator prey interactions, but also the behavioural ecology of both carnivores and primates independently.

Although 2nd order resource selection functions found that the neighbouring Blouberg mountains may have as suitable habitat for leopards, there has yet to be a formal assessment regarding habitat selection on a finer spatial scale (3rd and 4th order RSFS) in such populations. Such a comparative study between leopards in both western Soutpansberg and the neighbouring Blouberg mountains may indicate whether these populations are influenced similarly by specific environmental and anthropogenic variables. In addition, such research can also be extended towards assessing activity patterns in leopards residing in the Blouberg mountains as a means to not only assess whether such patterns are similar to leopards residing in the western Soutpansberg, but also if leopards residing in the Blouberg mountains shift their activity patterns when in anthropogenic habitats**.**

An additional avenue for future research involves implementing resource selection functions deriving from carnivores to assess perceived risk in other mammalian species. The combined implementation of both antipredator data derived from the prey, as well as the probability of encountering carnivores residing in the area, may permit a greater understanding of long term trends in behaviours such as spatial avoidance, vigilance, and vocalisations rather than the immediate effect after a direct encounter. Such an analysis may also aid in assessing how much of an understanding a prey species actually has regarding the whereabouts of their primary predators. The latter factor could be particularly compelling given that it is often assumed that prey have an imperfect knowledge of the whereabouts of their predators (Laundré, 2010).

Although baboons within the western Soutpansberg (and elsewhere) are occasionally predated on by leopards (Busse, 1980; Chase Grey, Bell and Hill, 2017; Williams *et al.*, 2018), it should be noted that they are not considered primary prey in themselves, with leopards preferring to target small to medium sized ungulates or smaller primates (Chase Grey, Bell and Hill, 2017). Given this, it would be interesting to know if the probability of directly encountering a carnivore (through resource selection functions) elicits a greater response in prey species that may suffer higher rates of predation from carnivore species that is also studied. In the context of primates in the western Soutpansberg, the

utilisation of leopard RSFs may be particularly interesting when assessing perceived risk in species that both have the ability to elicit predator specific calls, yet also experience different rates of predation (samango and vervet monkeys in particular). Such research would not only allow for one to assess if such predator-specific vocalisations are omitted in areas where their primary predators are likely to occur, but also if direct spatial avoidance is e likely to be more prevalent in species that are predated on more.

One interesting finding from this thesis regards the different behavioural strategies exhibited by baboons when faced with two different types of threats. In this case, the probability of encountering an ambush predator (the leopard) had the greatest effect on vigilance (with no effect on space use), whereas spatial avoidance was primarily utilised when faced with the threat imposed by other baboon groups. Given these findings, it would be interesting to assess how baboons residing in a multi-predator system must balance a combination between resource acquisition while simultaneously avoiding several predator species in addition to other groups.

For example, one can ask: do baboons spatially vary their avoidance strategies or vigilance levels when faced with cursorial predators (such as spotted hyaenas or African wild dogs) that do not rely on stealth? Cursorial predators are generally considered to be less predictable regarding where they hunt compared to ambush hunters that rely on habitat features when stalking prey (Schmidt and Kuijper, 2015). Therefore, it is has been hypothesised that predation cues from cursorial predators may also be less predictable compared to ambush predators (where risk can be associated with specific visual features) (Schmidt and Kuijper, 2015). Although leopard activity levels had no effect on baboon avoidance, alarm call distribution, or vigilance levels, it may be possible that primates (among other prey items) recognise spatial patterns in activity in predators that rely on pursuit (and a heavy expenditure of energy) when hunting (such as cursorial predators). Although there are several studies that provide evidence that prey may temporally avoid when their predators are active (Kotler *et al.*, 2002; Atwood, Gese and Kunkel, 2009; Tambling *et al.*, 2015) there are few studies that have assessed if such avoidance strategies also

apply to *where* they are active. Such prospective work has the potential to shed light regarding if recognised risk (and antipredator strategies utilised) may vary depending not only on the likelihood of encountering predators, yet also on the hunting method utilised by the carnivore itself.

Since baboons are most often at risk from ambush predators (such as large felids), it would be interesting to assess if the spatial patterns found here (increased vigilance, yet not spatial avoidance) are also found when faced with two species within the same study system that exhibit similar hunting strategies (such as lions and leopards) (Sunquist and Sunquist, 1989). If assessed, would one predator have a greater effect on space use or vigilance than the other? Likewise, would factors such as the presence of resources in high risk areas or possibly even differences in predator pressure influence such effects on baboon vigilance patterns?

It would also be important to assess how long and short term space use trends in response to other groups are also influenced by the presence of multiple predators on the landscape. In this instance, baboons would not only have to face the risk imposed by different species of predators yet may also have to simultaneously avoid intergroup encounters. Baboons residing in such conditions may therefore adopt additional strategies to maximise energy intake while simultaneously avoiding the risk imposed by different threats.

Finally, although using predator specific data to assess spatial patterns and avoidance strategies has the potential to provide an accurate understanding how prey items respond to the actual probability of encountering their predator, it should also be stated that as the focal group was habituated, it is possible that predation pressure may either be lower due to the presence of a human during the day (Isbell and Young, 1993a), or, that leopards will simply choose to primarily hunt baboons at night (Altmann and Altmann, 1973; Busse, 1980). As such, although behavioural observations (and as such, habituation) were required to assess spatial patterns in vigilance, they may not necessarily be needed when assessing spatial use alone, and in fact, may even lower the probability for baboons encountering leopards. Therefore, it is recommended that future studies should also consider the impact that habituation may have

and, as such, aim to study populations whose behavioural ecology (including predation risk) is not influenced by humans.

7.5 Conclusion

This is the first study that used a combination of long term spatial, activity, and behavioural data to assess the behavioural ecology of a predator (leopard), and its prey (chacma baboon) within the same environment (Although see Isbell *et al.*, 2018 for an assessement of short term risk of baboons from leopards). In addition, this is one of the few studies that have used data directly deriving from the principal predator to assess long term spatial trends in avoidance and vigilance of a prey species with the aid of spatial autoregressive models.

This thesis highlights the fact that both baboons and leopards alter their space use and activity levels throughout the landscape in response to abiotic, anthropogenic, and biotic conditions. In addition, it lends support that an understanding of the predator species is a fundamental (yet often forgotten) component in understanding the complex decision making processes required to maintain fitness through food acquisition while avoiding the risk imposed by specific threats.

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Appendices

Appendix 1: Chapter 2 Supplementary Material

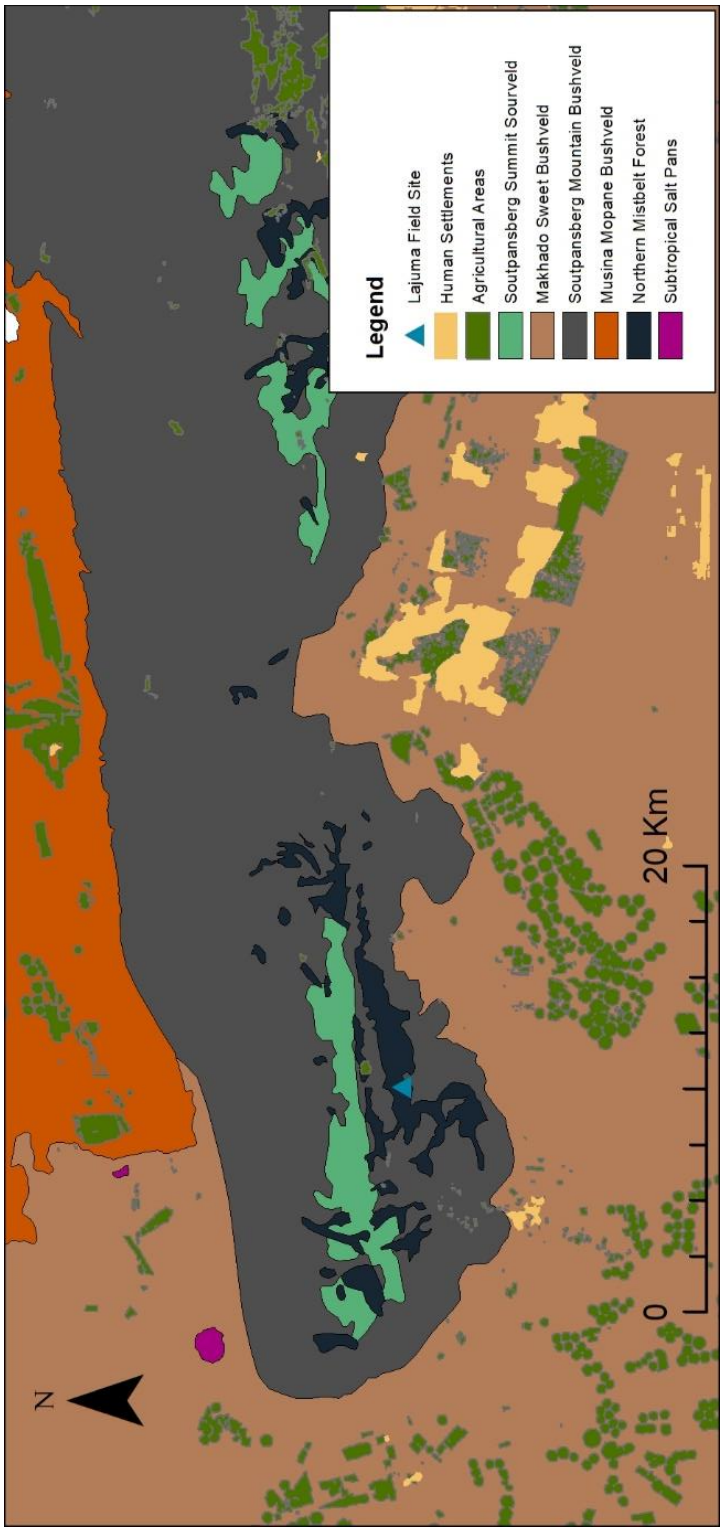

Figure S1.1 Categorical (vector) habitat types in the western Soutpansberg mountains.

Table S1.1 Plant species consumed by chacma baboons in the western Soutpansberg mountains.

Code	Scientific Nomenclature	Common Name
A.at	*Senegalia ataxacantha*	Flame thorn
A.ka	*Vachellia karroo*	Sweet thorn
A.si	*Vachellia sieberiana* var. *woodii*	Paper thorn
C.ed	*Carissa edulis*	Climbing num num
C.fa	*Capparis fascicularis*	Caper bush
C.mu	*Canthium mundianum*	Rock alder
C.sy	*Croton sylvaticus*	Forest fever berry
D.ci	*Dichrostachys cinerea* subsp. *africana*	Sickle bush
D.ge	*Drypetes gerrardii*	Forest iron plum
D.ze	*Dovyalis zeyheri*	Apricot sourberry
E.ca	*Ekebergia capensis*	Cape ash
E.ly	*Erythrina lysistemon*	Sacred coral tree
E.ma	*Englerophytum magalismontanum*	Stem fruit
F.bu	*Ficus burkei*	Common fig
F.cr	*Ficus craterostoma*	Forest fig
F.in	*Ficus ingens*	Red-leaved rock fig
F.su	*Ficus sur*	Broom-cluster fig
H.am	*Hyperacanthus amoenus*	Thorny gardenia
L.ca	*Lantana camara*	Tick-berry
L.dr	*Lagynias dryadum*	Woodland pendant medlar
M.ze	*Mimusops zeyheri*	Transvaal red milkwood
O.eu	*Olea europaea* subsp. *africana*	Wild olive
O.fi	*Opuntia ficus-indica*	Prickly pear cactus
P.af	*Peltophorum africanum*	African wattle
P.an	*Pterocarpus angolensis*	Bloodwood/teak tree
P.gu	*Psidum guajava*	Common guava
R.ca	*Rauvolfia caffra*	Quinine Tree
R.to	*Rhoicissus tomentosa*	Forest grape
S.ch	*Sersia chirindensis*	Red currant
S.co	*Syzygium cordatum*	Common water-berry
S.ge	*Syzigium gerradii*	Forest water-berry
S.le	*Syzygium legatii*	Mountain water-berry
S.lu	*Searsia lucida lucida*	Glossy crow berry
S.pe	*Searsia pentheri*	Crow-berry
Se.pet	*Senna petersiana*	Monkey pod
St.coc	*Strychnos cocculoides*	Corkey-barked monkey orange
T.dr	*Trichilia dregeana*	Forest mahogany
V.gl	*Volkameria glabra*	Smooth tinderwood
V.in	*Vangueria infausta*	Wild medlar
V.pa	*Vangueria parvifolia*	Mountain wild medlar
Z.mu	*Ziziphus mucronate* subsp. *mucronata*	Buffalo thorn

Appendix 2: Chapter 3 Supplementary Material

Table S2.1 Top ten candidate models for 2nd order resource selection functions.

Model	Deviance	AICc	BIC	Delta AIC
Aspect + Elevation + NDVI + Ruggedness + Slope + Human Settlements	13874	13906	14023	0.00
Aspect + Agricultural + Elevation + NDVI + Ruggedness + Slope + Human Settlements	13874	13908	14033	1.93
Aspect + Elevation + NDVI + Ruggedness + Slope + Human Settlements + Distance from Water	13874	13908	14033	2.00
Aspect + Agricultural + Elevation + NDVI + Ruggedness + Slope + Human Settlements + Distance from Water	13874	13910	14042	1.93
Aspect + Elevation + NDVI + Ruggedness + Human Settlements	13884	13914	14024	8.38
Aspect +Agricultural + Elevation + NDVI + Ruggedness + Human Settlements	13884	13916	14034	10.38
Aspect + Elevation+ NDVI+ Ruggedness+ Human Settlements + Distance from Water	13884	13916	14034	10.39
Aspect + Elevation+ NDVI+ Slope+ Human Settlements	13887	13917	14027	11.39
Aspect +Agricultural+ Elevation+ NDVI+ Ruggedness+ Human Settlements + Distance from Water	13884	13918	14043	12.39
Aspect + Elevation+ NDVI + Slope+ Human Settlements + Distance from Water	13887	13919	14037	13.36

Table S2.2 Top ten candidate models for 3rd order resource selection functions.

Top Model	Deviance	AICc	BIC	Delta AIC
Aspect + Elevation + NDVI + Human Settlements	15446	15474	15577	0.00
Aspect + Agricultural + Elevation + NDVI + Human Settlements	15444	15474	15584	0.16
Aspect + Agricultural + NDVI + Human Settlements	15446	15474	15577	0.22
Aspect + NDVI + Human Settlements	15449	15475	15570	0.69
Aspect + Agricultural + Elevation + NDVI + Slope + Human Settlements	15443	15475	15593	1.09
Aspect + Elevation + NDVI + Slope + Human Settlements	15445	15475	15585	1.22
Aspect + Elevation + NDVI + Ruggedness + Human Settlements	15446	15476	15586	1.55
Aspect + Agricultural + NDVI + Ruggedness + Human Settlements	15446	15476	15586	1.55
Aspect + Agricultural + Elevation + NDVI + Ruggedness + Human Settlements	15444	15476	15593	1.78
Aspect + NDVI + Ruggedness + Human Settlements	15448	15476	15579	1.85

Table S2.3 Top ten candidate models for 4th order resource selection functions.

Model	Deviance	AICc	BIC	Delta AIC
NDVI	1033	1041	1064	0.00
NDVI+ Human Settlements	1032	1042	1072	1.39
NDVI+ Agricultural	1033	1043	1072	1.91
NDVI + Ruggedness	1033	1043	1072	1.94
(Intercept)	1037	1043	1060	1.94
NDVI + Elevation	1033	1043	1072	1.98
NDVI + Distance from Water	1033	1043	1072	2.01
NDVI+ Slope	1033	1043	1072	2.01
NDVI+ Human Settlements + Elevation	1032	1044	1080	3.29
NDVI + Human Settlements + Ruggedness	1032	1044	1080	3.36

Table S2.4 Coefficients for top alternative (habitat) model for 2nd Order RSF (AIC = 14267).

Fixed Effects	**Estimate**	**Std. Error**	**z value**	**P Value**
(Intercept)	-1.85E+00	1.04E+00	-1.783	0.074
Aspect (E)	4.38E-01	5.55E-01	0.788	0.430
Aspect (N)	7.11E-01	5.54E-01	1.282	0.199
Aspect (NE)	6.26E-01	5.56E-01	1.126	0.260
Aspect (NW)	6.13E-01	5.55E-01	1.105	0.269
Aspect (S)	9.40E-01	5.53E-01	1.7	0.089
Aspect (SE)	7.18E-01	5.53E-01	1.297	0.194
Aspect (SW)	1.03E+00	5.54E-01	1.849	0.064
Aspect (W)	9.38E-01	5.56E-01	1.685	0.092
Elevation	-1.24E-03	1.66E-04	-7.47	**<0.001**
Habitat (Makhado Sweet Bushveld)	3.49E-01	8.51E-01	0.41	0.681
Habitat (Musina Mopane Bushveld)	-1.73E+00	1.05E+00	-1.647	0.099
Habitat (Northern Mistbelt Forest)	2.84E+00	8.56E-01	3.321	**0.000**
Habitat (Soutpansberg Mountain Bushveld)	2.01E+00	8.54E-01	2.35	**0.018**
Habitat (Soutpansberg Summit Sourveld)	7.62E-01	8.64E-01	0.882	0.377
Ruggedness	8.22E+00	4.66E+00	1.765	0.077
Slope	5.20E-03	2.75E-03	1.891	0.058
Distance from Human Settlements	8.07E-05	8.37E-06	9.633	**<0.001**
Distance from Distance from Water	9.22E-05	3.69E-05	2.5	**0.012422**

Table S2.5 Coefficients for top alternative (habitat) model for 3rd Order RSF (AIC = 15635).

Fixed Effects	Estimate	Std. Error z	Value	P Value
(Intercept)	-2.26E+00	1.30E+00	-1.735	0.082
Aspect (E)	-1.44E-01	7.66E-01	-0.187	0.851
Aspect (N)	3.18E-02	7.66E-01	0.042	0.966
Aspect (NE)	1.45E-02	7.67E-01	0.019	0.984
Aspect (NW)	2.02E-01	7.66E-01	0.264	0.791
Aspect (S)	1.43E-01	7.65E-01	0.187	0.851
Aspect (SE)	-5.25E-02	7.65E-01	-0.069	0.945
Aspect (SW)	2.41E-01	7.65E-01	0.315	0.752
Aspect (W)	4.10E-01	7.67E-01	0.534	0.593
Distance from Agricultural Areas	4.51E-05	2.28E-05	1.981	**0.047**
Habitat (Makhado Sweet Bushveld)	2.02E+00	1.05E+00	1.919	0.054
Habitat (Musina Mopane Bushveld)	1.59E+00	1.21E+00	1.315	0.188
Habitat (Northern Mistbelt Forest)	2.58E+00	1.06E+00	2.435	**0.014**
Habitat (Soutpansberg Mountain Bushveld)	2.41E+00	1.06E+00	2.279	**0.022**
Habitat (Soutpansberg Summit Sourveld)	1.73E+00	1.06E+00	1.626	0.103
Distance from Human Settlements	3.76E-05	9.35E-06	4.017	**<0.001**
Elevation	-4.79E-04	1.56E-04	-3.063	**0.002**

Table S2.6 Coefficients for top alternative (habitat) Model for 4th Order RSF (AIC = 1043).

Fixed Effects	**Estimate**	**Std. Error**	**z value**	**P Value**
(Intercept)	-2.99573	0.09022	-33.2	**<0.001**

Appendix 3: Chapter 4 Supplementary Material

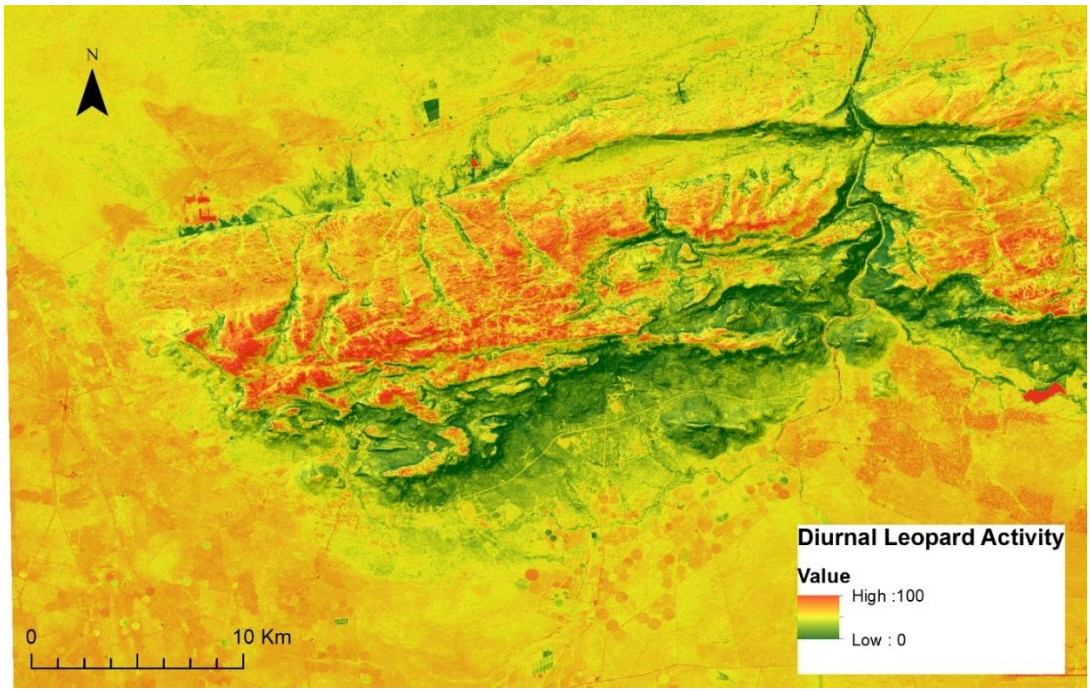

Figure S3.1 Projected diurnal leopard activity levels across the western Soutpansberg.

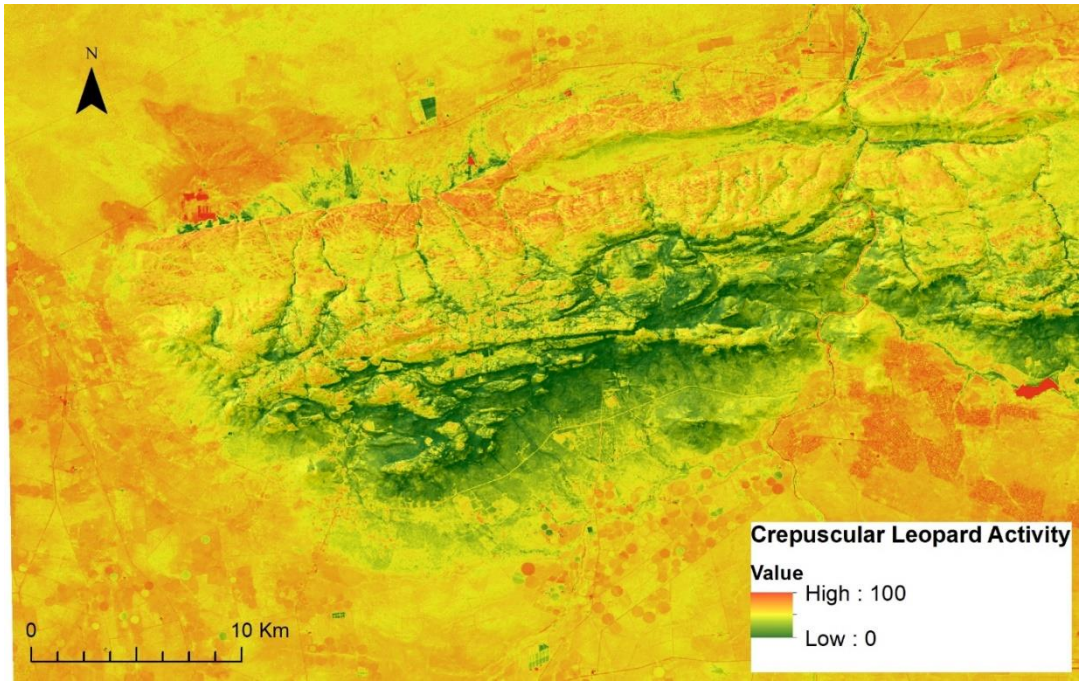

Figure S3.2 Projected crepuscular leopard activity levels across the western Soutpansberg.

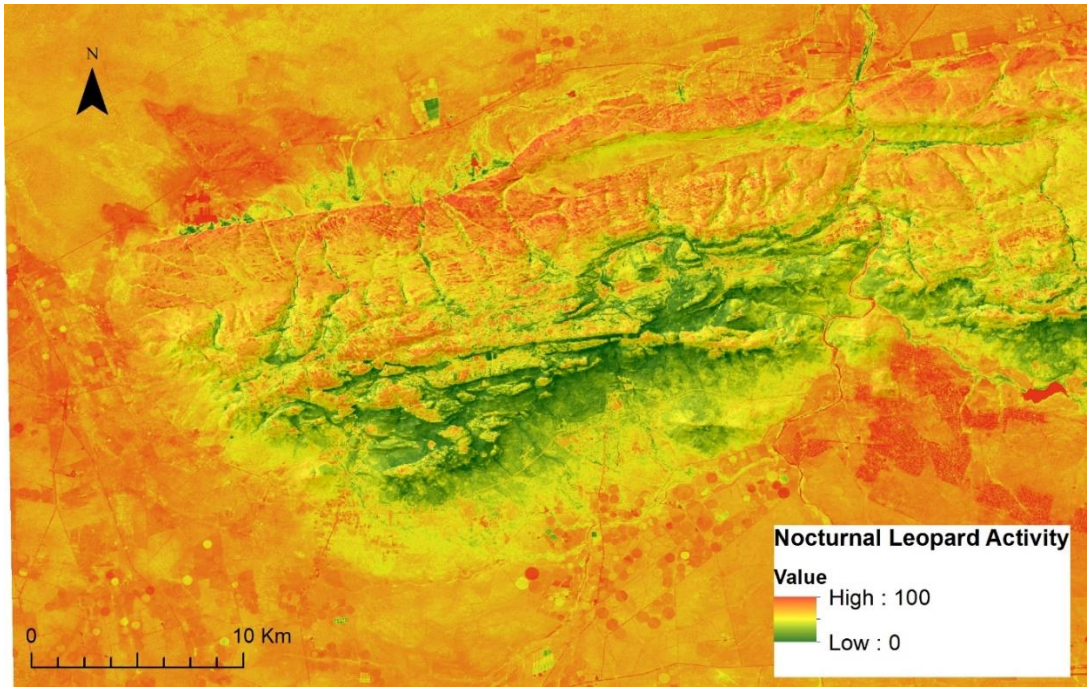

Figure S3.3 Projected nocturnal leopard activity levels across the western Soutpansberg.

Appendix 4: Chapter 5 Supplementary Material

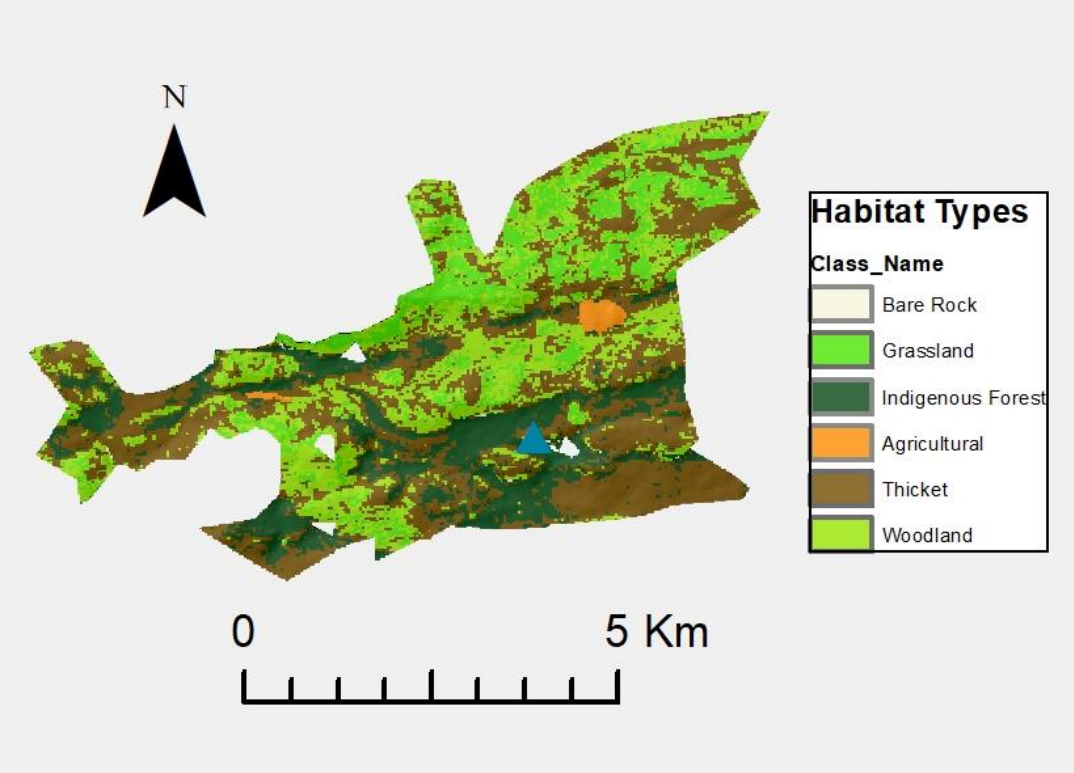

Figure S4.1 Habitat (raster) types found within the baboon utilisation distribution.

Table S4.1 Annual average food availability per raster habitat type.

Habitat	Value	N
Indigenous Forest	269.889	316
Thicket	269.478	244
Woodland	109.265	145
Grassland	110.314	69
Agricultural	8.173	16
Bare Rock	0	3

Table S4.2 Average summer food availability per raster habitat type.

Habitat	Value	N
Indigenous Forest	370.785	316
Thicket	506.557	244
Woodland	202.577	145
Grassland	284.659	69
Agricultural	0	16
Bare Rock	0	3

Table S4.3 Average winter food availability per raster habitat type.

Habitat	Value	N
Indigenous Forest	68.341	316
Thicket	73.972	244
Woodland	14.114	145
Grassland	0	69
Agricultural	20.785	16
Bare Rock	0	3

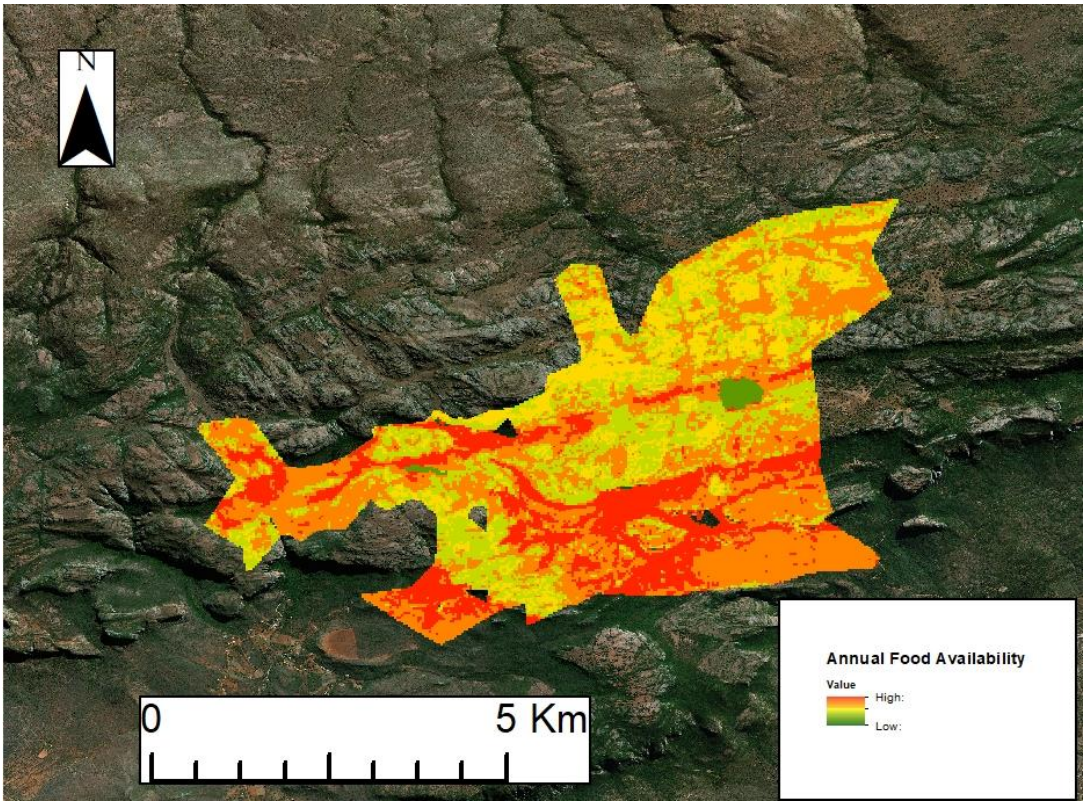

Figure S4.2 Average food availability annually and per season.

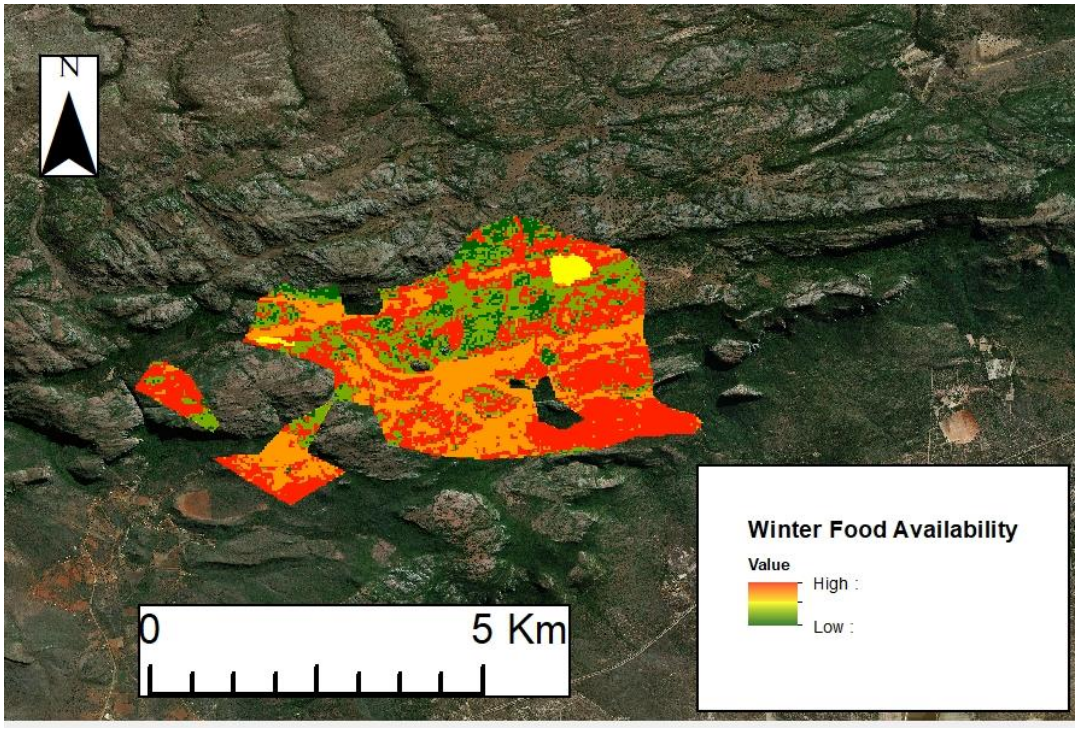

Figure S4.3 Average winter food availability.

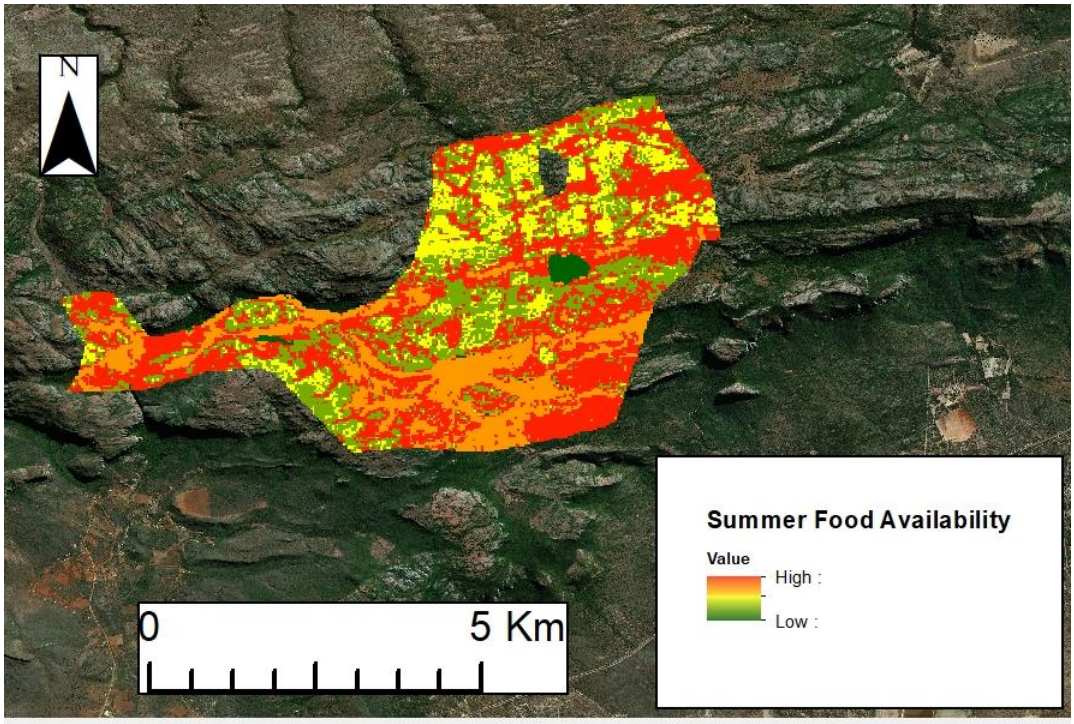

Figure S4.4 Average summer food availability.

Table S4.4 Moran's I value for every variable utilised per dataset.

Dataset/Variable	Moran's I Value
Annual (Dataset A)	
Distance to Water	0.510
Distance to Sleeping Site	0.982
99% Annual Utilisation Distribution	0.836
Probability of Intergroup Encounter	0.518
Leopard Resource Selection Functions	0.536
Food Availability	0.380
Landscape of Fear	0.392
Winter (Dataset B)	
Distance to Water	0.530
Distance to Sleeping Site	0.934
99% Annual Utilisation Distribution	0.806
Probability of Intergroup Encounter	0.708
Leopard Resource Selection Functions	0.505
Food Availability	0.377
Summer (Dataset C)	
Distance to Water	0.571
Distance to Sleeping Site	0.983
99% Annual Utilisation Distribution	0.916
Probability of Intergroup Encounter	0.813
Leopard Resource Selection Functions	0.495
Food Availability	0.217
Vigilance (Dataset D)	
Percent Vigilant	0.031
99% Annual Utilisation Distribution	0.779
Probability of Intergroup Encounter	0.268
Leopard Resource Selection Function	0.215

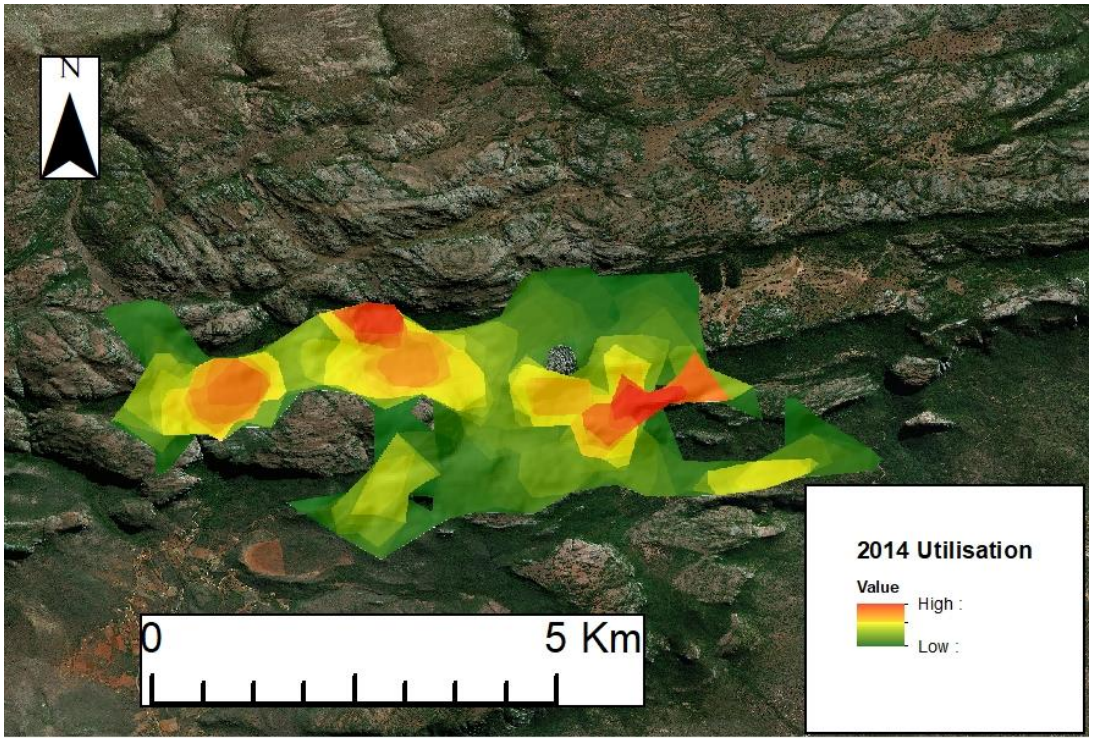

Figure S4.5 Utilisation distribution for focal group in 2014.

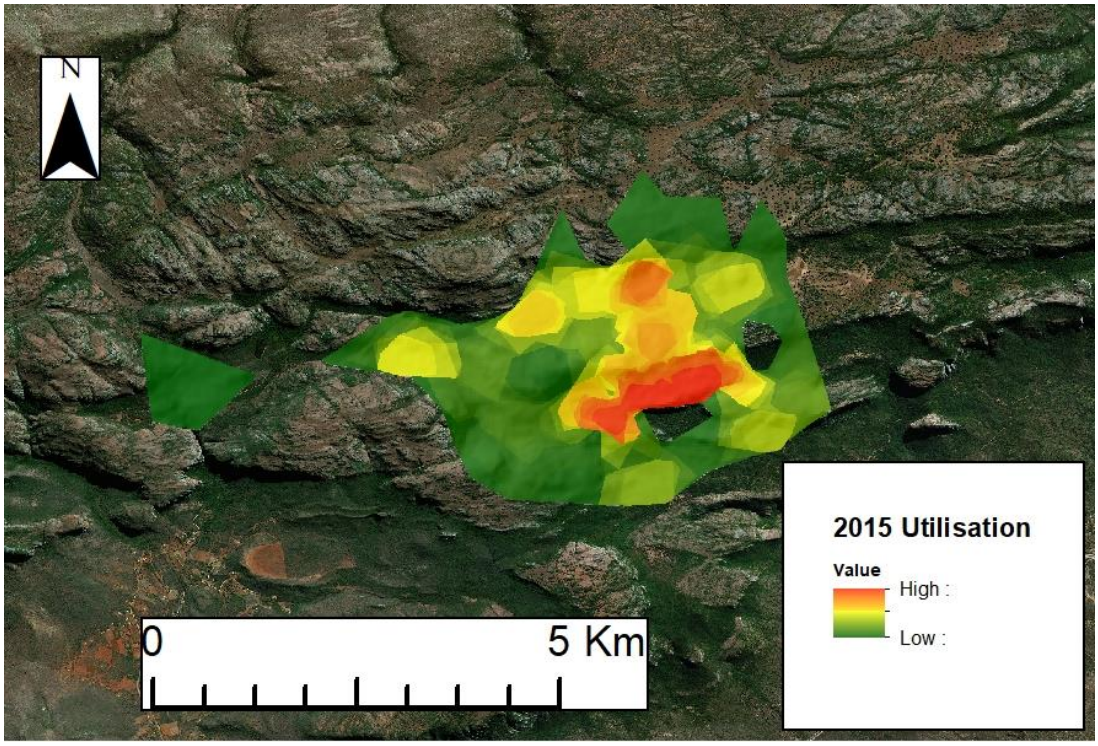

Figure S4.6 Utilisation distribution for focal group in 2015.

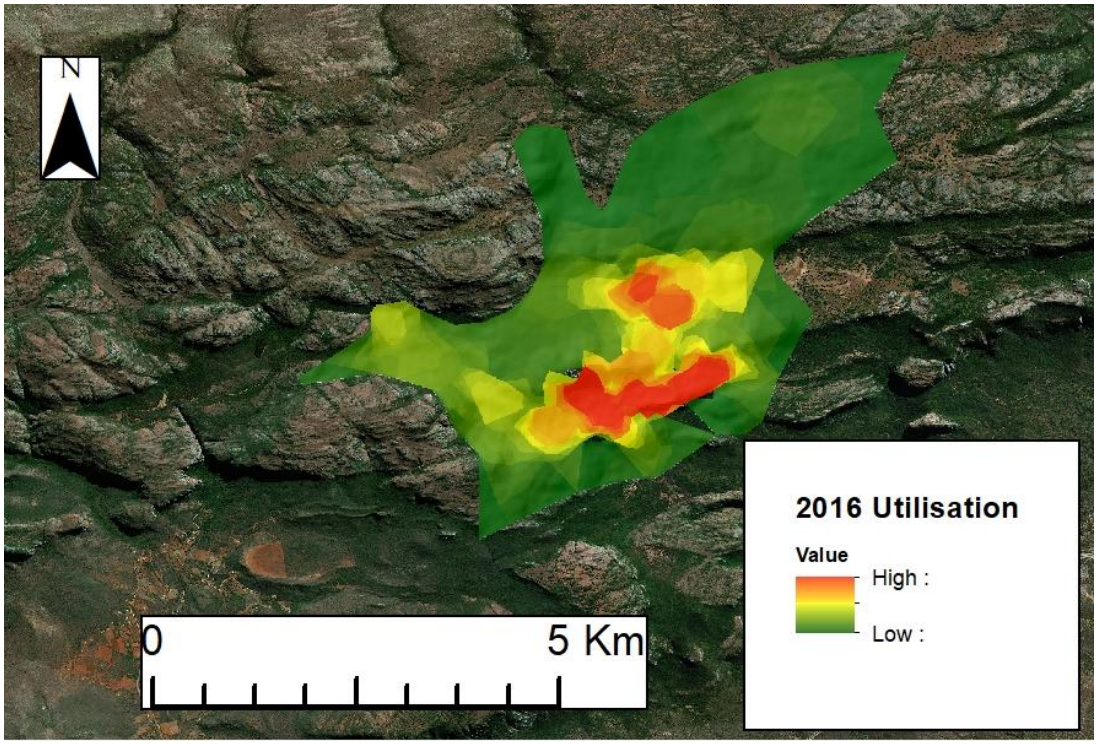

Figure S4.7 Utilisation distribution for focal group in 2016.

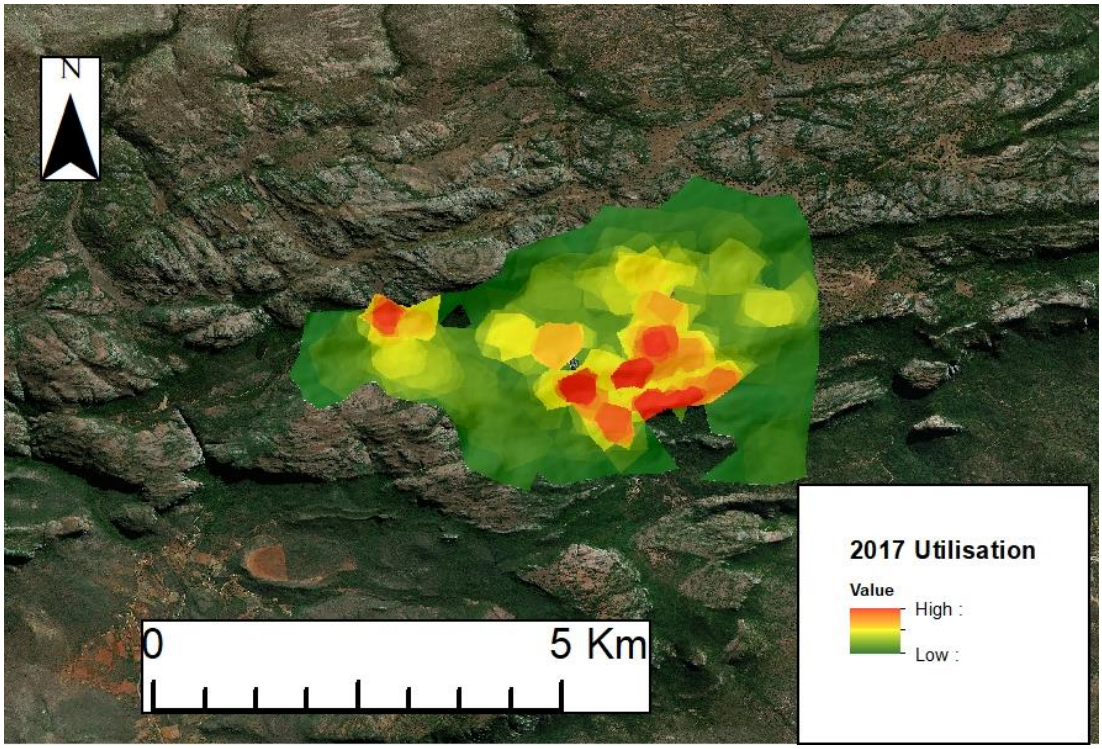

Figure S4.8 Utilisation distribution for focal group in 2017.

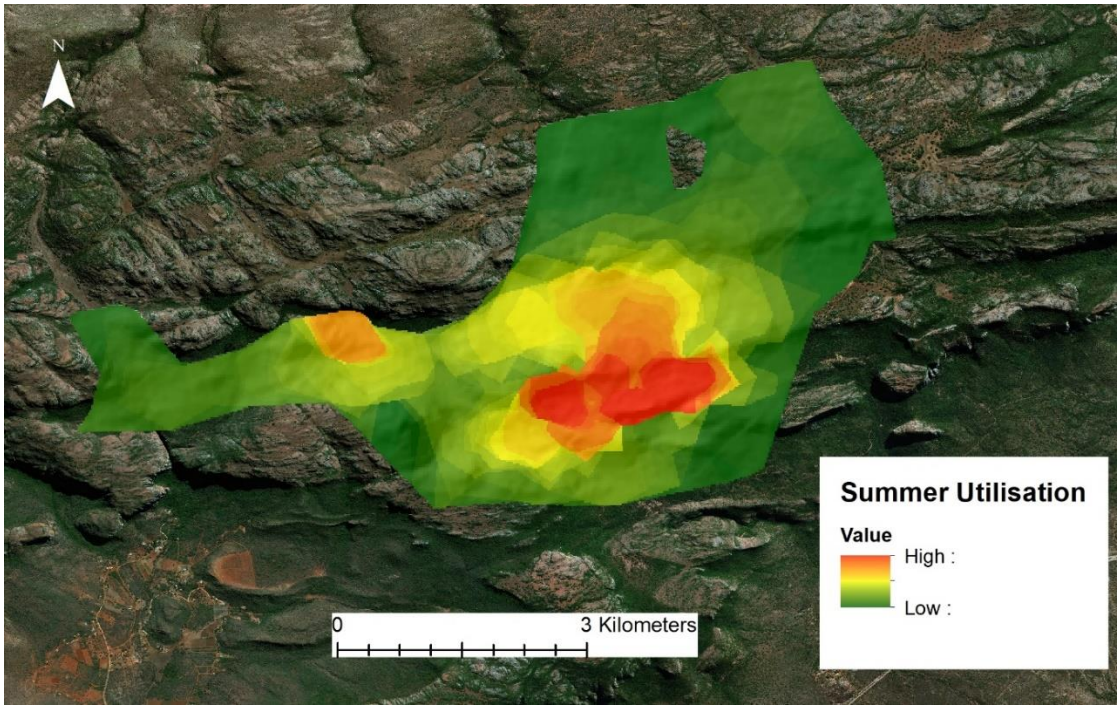

Figure S4.9 Summer utilisation distribution of focal baboon group.

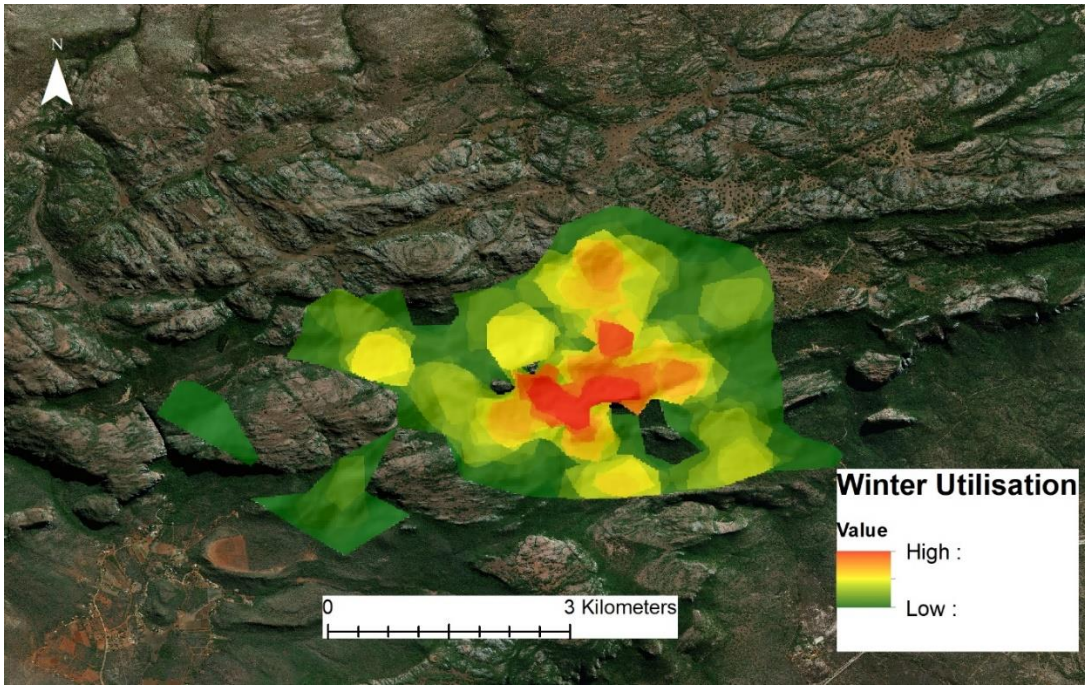

Figure S4.10 Winter utilisation distribution of focal baboon group.

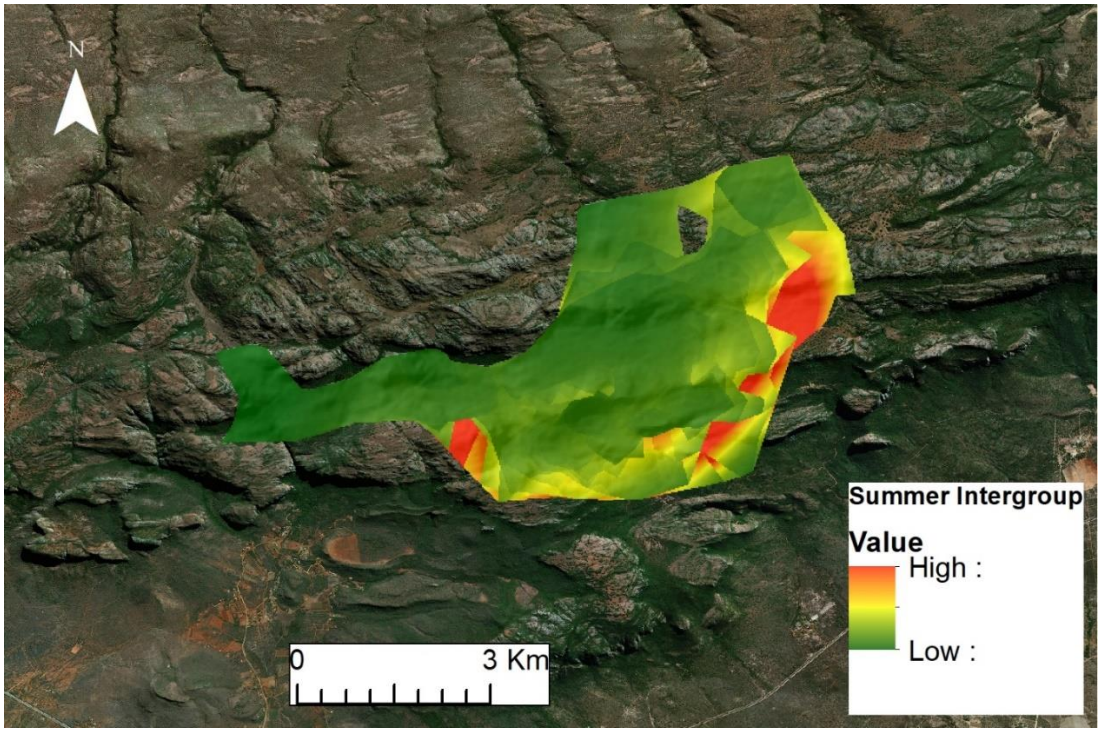

Figure S4.11 Probability of encountering other baboon groups in summer.

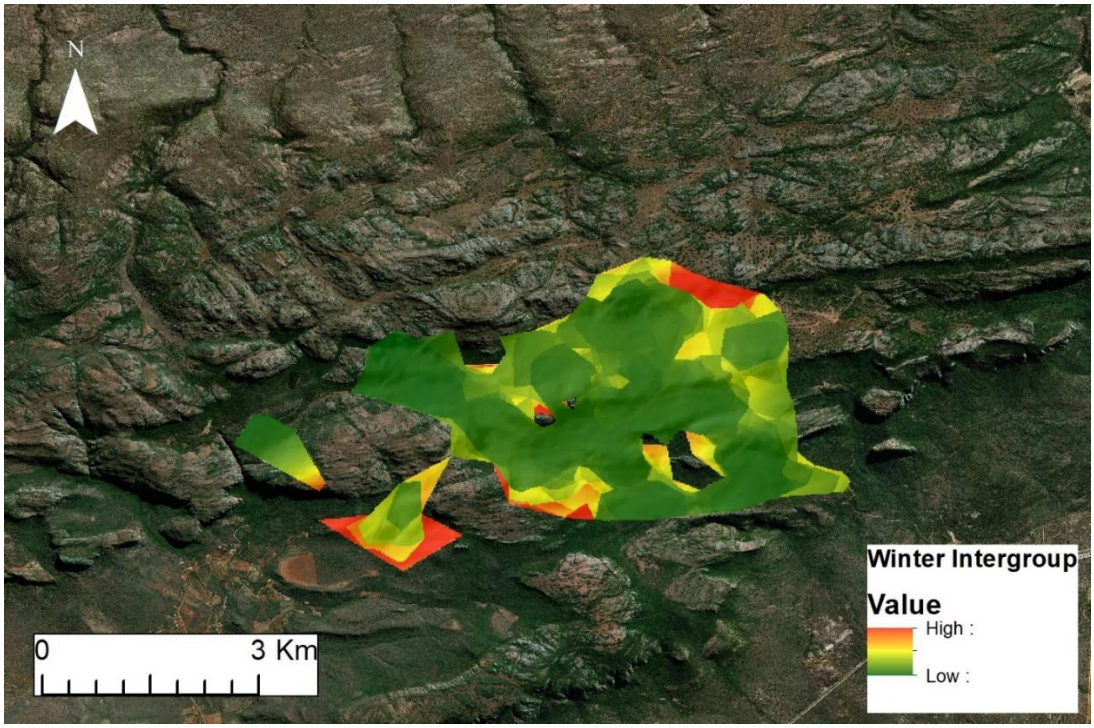

Figure S4.12 Probability of encountering other baboon groups in winter.

Appendix 5: Primate Predator Project's Baboon Protocol

Background information

Chacma baboons (*Papio hamadryas ursinus*) are located primarily in Southern Africa, and are distributed across Botswana, South Africa, Mozambique, Zimbabwe, Angola, Namibia and Zambia. They are the largest baboon subspecies and are a primarily terrestrial primate. According to the IUCN red list, baboons are currently of least concern. However, a rapidly growing human population has increased contact between humans and baboons. This has lead to escalated hunting, killing, and snaring of baboons. Development of agriculture in Southern Africa has also lead to a treacherous interest in crop raiding. Due to these human-baboon conflicts, baboons are viewed as vermin across Southern Africa.

Baboons are often known as the "adaptable monkey," meaning that they can live in a wide variety of different habitats. These include semi-arid deserts, tropical forests, savannas, open woodlands, and mountainous environments. A reliable water source and safe sleeping sites are the major requirements for a baboon‟s habitat. This troop of chacma baboons, known as the House Troop, inhabits an afromontane habitat. Approximately 80 individuals reside in this troop and each individual can be distinguished based on unique characteristics.

More information can be found on the IUCN red list website (http://www.iucnredlist.org/details/16022/0).

Your responsibilities

As a baboon research volunteer you will have a range of different responsibilities. Your main responsibility will be helping to complete our baboon follow days. Each month we aim to complete a minimum of 8 dawn-dusk follow days with our habituated group. During these follow days we attempt to collect data using one of two methods, scan sampling and focal sampling. Another important responsibility will be helping to complete our vegetation sampling. This will involve collecting data from our phenological transects and through vegetation plots, we aim to complete 15 vegetation plots each month. All of these responsibilities will be explained to you in more detail by the Primate Coordinator.

Rules towards the monkeys

In respect of the monkeys and for your safety, we ask you to adhere to the following rules when in the presence of the baboons.

Do not feed the monkeys. This includes throwing waste food into the forest. Human food can make the monkeys ill and also causes them to associate humans with food, this can lead to them becoming aggressive in the future.

Be inconspicuous with your food. This applies both in the field and at camp. Whenever possible try not to eat food within sight of the monkeys (try to hide behind vegetation). When in camp ensure that no food is left outside and if possible store all food within cupboards or fridges.

Do not leave your belonging unattended.

Do not touch or attempt to touch the monkeys. We are a neutral presence and these are wild animals who do not want to be touched. They may respond aggressively and should a monkey attack a human that individual may have to be put down.

Avoid eye contact. Eye contact is an aggressive dominant behaviour in baboons, so please don‟t stare at any individuals for long periods of time.

Be as quiet as possible. The baboons will be prefer it if researchers walk/talk as quietly as possible during a follow day.

Safety recommendations

A minimum of 2 people are required on a baboon follow day. Ensure all researchers have 2 fully charged radios with them before beginning the day.

Due to the cliffs, radios do not always work. Therefore, please take a mobile phone with you. The emergency code is 112 and we also suggest you store the numbers of a few members of the team, especially Ian.

Always take a GPS which has the camps marked on it, should you need to quickly find people.

Many of the rocks in Lajuma have lichen growing on them, which when wet becomes very slippery. Be aware of this if it has been raining or if it is misty.

If a thunderstorm is approaching find shelter in one of the camps, even if this means ending your follow day (only applies if the storm is near/above you).

You will leave the monkeys at dusk and may be several km from camp. Always therefore ensure you take a torch with you as you will have to walk back in the dark.

We recommend taking a minimum of 3 litres of water (4 on a hot day). This is not just for drinking, but may be important for first aid reasons (e.g. problem with spitting cobra).

DO NOT PUT YOURSELF AT RISK. Please don‟t attempt to follow the monkeys through terrain you are not comfortable with.

Equipment

PDA

When in the field please use one of the PDA covers. The cover will only protect against very light rain. In heavier rain please try to keep the PDA within waterproof clothing as much as possible.

To access the data collection spreadsheet:

Press “Start” (Windows icon)

Press “File Explorer” (Folder with a magnifying glass icon)

Press Baboon scans template should appear

The baboon spreadsheet has 3 different tabs: Scan, Ad libitum, Codes.

There is an occasional problem with the spreadsheet where the sheet suddenly becomes too full or the options at the top disappear. If this happens tap the keyboard icon (bottom right) twice, and it should return to normal.

GPS

Familiarise yourself with the GPS. The most important function will be “Mark” which you will need to mark locations for the behavioural sampling.

To find the dawn and dusk times go to the Calendar option and they will be listed.

Please make sure that the GPS is set on Decimal Degrees. To do this go to the main menu and select “Setup, then “Units” and it is the top most option “hddd.ddddd”

If you require help with any of the equipment or the software we use, please see the Primate Coordinator.

Data collection

Finding the troop

The night before a follow day find the troop. GPS waypoints of sleeping sites are all recorded on baboon GPSs and a waypoint file exists on the Primate Hard drive named „baboon sleeping sites frequent‟ in the Masterfiles folder. You can see the sleeping sites mapped out on this and there are also direction and tips for reaching the more remote ones.

Below are some of the most common sleeping sites for the baboons:

Sleeping Site 1 – Cliffs above Ian‟s house and at Lookout.

Sleeping Site 2 – Cliffs South of where the Leopard and Klipspringer trails meet (Above the Barn).

Sleeping Site 3 – At the diagonal rock, before the Leopard trail leads into the bush.

Sleeping Site 4 – Cliffs East of the Leopard trail chimney into Ottosdahl.

Sleeping Site 5 - Cliffs behind Oldrich and Judy‟s house. Follow the trail behind house for about 200 meters, the sleeping site is south of the trail, on cliffs just past a plateau.

Sleeping Site 6 – Cliffs below Wilderness Camp.

Sleeping Site 7 – Porcupine trail sleeping site.

Sleeping site 8: In Ottosdahl, above field.

Sleeping site 9: Bergplaas cliffs. Large sleeping site, baboons often very spread out across these cliffs.

Sleeping Site 10a and 10b: Diepkluf, cliffs behind and west of rondervaals; take St.13 trail.

Sleeping Sites 11/12: Sigurwana sleeping sites. Baboons can be followed here but it is too far to reach the next day.

Sleeping Sites 13/14: 14 is in the big gorge at Ont Moet, 13 is on the cliffs above the road.

Sleeping site 15: Buysdorp near Camera Station 12.

Sleeping Site 16: This sleeping site is far into Buysdorp. Baboons can be followed here on a follow day but it is not safe to try to reach them there the next morning as there is not trail and the bush is very thick.

Sleeping Site 17: This is in a property called Scott. The baboons only went here once during a thunderstorm and hopefully won‟t go back again. Again it is to distant and inaccessible to reach.

Waypoints for locations of all these sleeping sites are located on the primate hard drive in the baboon research file in a mapsource file labelled „baboon sleeping sites frequent‟. There are top and bottom locations for most of them and also marked are trails to get to the top and bottom of SS9 in Bergplaas, SS13&14 in Ont Moet and SS15 in Buysdorp. In the morning you must arrive at the sleeping site a minimum of 10 minutes before dawn. We use the dawn dusk times found in the calendar of the Garmin

GPS. On misty days, the baboons often start moving later than on sunny days. Keep this in mind for finding them on these days.

Scan sampling

We currently perform scan samples every 10 minutes (at 00, 20 and 40 minutes past the hour). Each scan should last a maximum of 10 minutes, where you aim to sample as many individuals as possible. Please try to ensure you don‟t sample the same individual twice in one scan sample.

With each different scan sample please try to move about the group. This is to ensure you are not sampling the same individuals each time.

Just before the scan sample time you can fill out the first bits of information within the “Scan” tab. These are:

Date – Stick to the format DD/MM/YYYY (this is extremely important!)

Observer – Your name

Time – Write the appropriate time.

Weather:

S – Clear sky

S/C - <50% cloud cover

C/S - ≥50% cloud cover

C – 100% cloud cover

M - Mist

LR – Light rain

HR – Heavy rain

Wind:

C – Calm

B – Light breeze (leaves moving)

W – Windy (twigs and small branches moving)

VW – Very windy **(**larger branches moving)

Scan comments – Anything that might affect the group‟s behaviour.

In addition to the information recorded in the spreadsheet, you have to **MARK A WAYPOINT ON THE GPS FOR EACH SCAN.** The waypoint should be named in the follow way: Time (4 digits, no spaces, no colon), space, Date (day with 2 digits, month with first 3 letters in capitals, last 2 digits of year), space, first letter of group name. For example: 0615 25SEP13 B.

REMEMBER TO HIT OK AFTER TYPING THE WAYPOINT NAME OTHERWISE IT WON‟T SAVE!

Then you can proceed with the scan. It is important that you **do not** sample the same individual more than once in a sample. Try to be aware of which individuals you have already sampled. You can record data on individuals which weren‟t visible at the start of the scan but do not do so until they have been in sight for at least 15 seconds. You can also move around during the scan to try to sample as many individuals as possible, but again, for newly found individuals allow 15 seconds. This reduces the potential for bias of locomotive behaviours.

Listed below are the data you must record for each individual during a scan sample:

Age-sex class

This will be difficult at first to distinguish, and takes some practice. If you are struggling the Primate Coordinator may be able to give you some tips. The categories are:

AM (Adult male) – All secondary sexual characteristics fully grown, musculature (most noticeably in chest and rump) expands to full adult size.

AF (Adult female) – Attainment of full body size, either cycling regularly, pregnant or lactating. Nipples also enlarge and elongated from suckling infants.

ADM (Adolescent Male) – Massive growth in secondary sexual characteristics; testes expand, canines and mane grow longer, body size increases to near that of an adult male.

ADF (Adolescent Female) – Nearly adult female size, with the onset of the first sexual swellings. If visible, nipples are much smaller and button-like than that of an adult female.

J3M (Juvenile 3 **Males Only**) – Body size that of an adult female, muzzle further extended to nearly that of an adult male. Testes start to expand and are clearly visible. Mane becomes noticeable.

J2M/F (Juvenile 2) – Little demarcation from previous period, with greater body size. Hair becomes darker, changing to a more adult grey/brown colouration

J1M/F (Juvenile 1) – Little demarcation from previous period, but fully weaned and nutritionally independent. Muzzle starts becoming more elongated and pronounced. Pelage is still lighter than in adults.

INF2M/F (Infant 2) – Pelage fully yellow/brown. Ears and muzzle are completely grey. Nutritionally dependent on lactating mother, but undergoing weaning.

INF1M/F (Infant 1) – Pelage initially black, transitioning to yellow/brown. Ears and muzzles turning from pink through to gray. Nutritionally dependent on lactating mother.

 If unsure of an infant or juvenile‟s sex put „unk‟ after the age class e.g. J1UNK, INF2UNK.

UNK – unless completely sure of an individual ID write „unk‟ (unknown) in column for individual.

Habitats

WO (woodland): Woodland: can see sky overhead,; canopy is more open; allows sunlight to penetrate between the trees, limiting shade. Woodlands may support an understory of shrubs, herbs, or grasses. Mostly consists of acacia.

FO (Forest): largely closed canopy; trees tall; the branches and foliage interlock overhead to provide extensive and near continuous shade

RD (Road): Self explanatory

RO (Rocks): area where ground predominantly consists of rocks and boulders, rather than dirt.

FM (Farm): self explanatory. Ottosdal Macadamia farm or area around Ottosdal Farm House.

BU (Bush): area where shrubs are the dominant vegetation. A shrub is a woody perennial plant,

smaller than a tree, with several major branches arising near the base of the stem.

GR (Grassland): a large, open area covered predominantly with grass.

MA (Marshland): vegetation components of marshlands include reeds, sedges, and grasses. Exclusively found in flat regions along permanent water streams on peat.

Activity

For each individual record the first activity lasting at least 5 seconds.

F (Feeding) **–** Searching for, processing or injecting food

M (Moving) – Moving without any obvious sign they are searching for food

S (Socialising) – Any social activity, e.g. fighting, playing, being groomed by another

R (Resting) **–** Sitting, lying or standing, without engaging in any specific behaviour

OT (Other) – Any other activity, e.g. drinking, self play.

Qualifier

Each activity type has qualifiers which will allow you to more precisely define the activity.

Feeding - searching for, processing, or ingesting food.

Fe (Feeding) **–** Chewing, processing or ingesting food. You will need to further record **Food Item** and **Plant Species** where possible.

Fo (Foraging) – Actively searching for food that is not obvious without ingesting anything (putting anything into their mouth). A forage must last 5 seconds or more for the behaviour to be recorded as a forage.

Fcp (cheek pouch) – Feeding from food items stored in cheek pouches.

Moving – locomotion on ground, bush or tree for 5 seconds or more, without picking up any food items.

Wa (Walking) – Always 3 limbs touching the ground. Also applies to slow climbing.

Ru (Running) – Fewer than 3 limbs always touching the ground. Again, applies to fast climbing.

Socialising - includes grooming, play, affiliation, mating, and aggression. All of these behaviours have recipients (individual receiving the behaviour) that must also be recorded in addition to the recipient‟s activity.

Gg (Grooming given) – The individual is grooming another individual. In this case, the individual receiving the grooming should be recorded under “recipient” and “recipient behaviour”.

Gr (Grooming received) – The individual is being groomed by another individual. The individual performing the grooming should then be recorded under “recipient” and “recipient behaviour”.

Pl (Play) – Individual involved in social play (this differs from environmental play, which is not recorded).

Ag (Aggression) – Individual involved in an aggressive display as the aggressor.

Su (Submission) – Submissive in an aggressive display

Ma (Mating) – Self explanatory (although make sure it isn‟t just a mount-dominance

display)

Resting - individual is sitting, laying, or standing without performing any other activity for 5 seconds or more.

Rs (Resting sitting) – Individual is stationary while sitting without performing any other activity.

Rst (Resting standing) – Individual is stationary while standing without performing any other activity.

Rl (Resting lying) – Lying down

Rh (Resting huddled) – Huddling with other individuals

Sg (Self-grooming) – Grooming itself, also referred to as autogrooming.

Other

Ot (Other) – Write in “comments” what was observed

Dr – drinking

 If a female is carrying/suckling an infant record this in the comments box.

Recipients Activity – If involved in a social activity, put here the partner. Will usually be the sex-age class. Also a place for individual ID if known. If not, fill in with (UNK) “unknown”.

Plant species – Only put here if you are sure of the plant species being consumed. Once sure of the plant species, you will then enter the part of the plant that is being consumed in the **Food Item** category.

Trees

A.at- Acacia ataxacantha. Flame thorn

A.ka- *Acacia karoo.* Sweet thorn

A.si- Acacia sieberiana. Paper thorn

C.mu- Canthium mundianum. Rock alder

C.af- *Celtis africana.* White stinkwood

D.ze- *Dovyalis zeiheri.* Apricot sourberry

E.ca- Ekebergia capensis. Cape ash

E.ma- Englerophytum magalismontanum. Stem fruit

E.tr- Erytrococca trichogyne. Twin red-berry

E.ly- *Erythrina lysistemon.* Sacred Coral Tree

F.bu- *Ficus burkei.* Common fig

F.cr- Ficus craterostoma. Forest fig

F.su- *Ficus sur.* Broom-cluster fig

H.am- Hyperacanthus amoenus. Thorny gardenia

M.ze- *Mimusops zeiheri.* Transvaal rel milkwood

O.eu- *Olea europaea.* Wild olive

R.to- Rhoicissus tomentosa. Forest grape

R.ca- *Rauvolfia caffra.* Quinine tree

R.ch- Rhus chiridiensis. Red currant

R.pe- Rhus pentheri. Crowberry

S.co- *Syzygium cordatum.* Common waterberry

S.le- *Syzygium legatii.* Mountain waterberry

T.dr- Trichilia dregeana. Forest mahogany

Z.mu- Ziziphus mucronata. Buffalo thorn

OT (Other species) – If it is not one of these species and you can ID it then put the species

in the comments section. If you cannot ID it, collect a sample

and try to ID it later.

Grasses – being updated (see ground vegetation list on hard drive)

Other - other plant species baboons regularly feed on (see ground vegetation list on hard drive).

O.fi – *Opuntia ficus indica.* Prickly pear cactus.

M.se – *Mundulea sericea.* Cork bush.

D.vi – *Dioscorea villosa.* Wild Yam.

A.ha – *Aloe hahnii.* Aloe vera.

P.an – *Pterocarpus angolensis*. Wild Teak tree or Bloodwood.

Food item

FR – Fruit

SE – Seeds, includes *Acacia* seed pods

FL – Flowers

LE – Leave of trees and bushes

LL – Leaf litter, but cannot tell what item

GR – Plants without bark and with parallel venation on leaves (grasses)

HE – Plants without bark and without parallel venation on leaves (herbs)

RO – Underground roots

BK – Bark

INV – Invertebrates

UNK – Unknown

OT – Other, put what item in comments, e.g. milk suckling

Height from ground – To the nearest metre. There is a code >10 for anything higher than 10m

Vigilance – Is the animal looking around?

NT – Not vigilant

LU – Looking upwards

LD – Looking downwards

SC – Scanning in a horizontal plane

ME – Looking at the observer

SO – Social vigilance, looking at another monkey

OT – Other (e.g. looking at a different species)

UNK – Unknown

Number of nearby individuals (nearest neighbours) – Number of individuals within 5m of the focal individual (does not include dependent infants).

After completing the information for each individual, **you have to copy and paste the general information to all the individuals of that particular scan**. After this, make sure you have saved the spreadsheet.

Focal Sampling

For focal sampling, you must follow one individual for 10 minutes. A seven-minute rule has been put in place where if you lose the individual after seven minutes you may keep the focal. Record each instance of a change in behaviour. For example, if a baboon feeds, then walks, then grooms, then rests, there should be four behaviours in the focal. However, if a baboon spends all ten minutes walking, there should only be one behaviour included in the entire focal. In order to record focals, you must first be able to tell the individuals in the troop apart from each other. This is because for each focal, you must record:

Age-sex class (same as for scans)

Individual

Activity and sub-activity (same as scans)

Neighbours ASC and ID (all individuals that are within 5 meters of the focal individual)

Ad libitum sampling

Not all relevant data can be collected using the scan samples, so there are certain behaviours we record as and when they happen (*ad libitum*). There is a separate tab in the spreadsheet for such recordings.

The following categories are used:

V – (vocalisation):

A - Alarm call

WH – Wahoo – call used in male dominance displays

L – Lost calls, made when group is separated

OT (Other) – Any other relevant vocalisation

E - (Encounter):

IE (Inter-specific encounter) – The presence of members of another species within 10m of an individual from the troop. Do not count domestic animals/people unless the monkeys are seen to react to their presence. If they are present during a scan, then that information should also go in the scan comments section.

WE (Within-specific encounter) – Interactions with another group. Record all details in the comments section

BE - (Behaviour)

AG (Aggression) – Aggressive encounters involving more than one individual. Record details of the encounter, including age-sex classes, in the comments.

MA (Mating) – If you see mating (even if recorded in the scan) put details of it here

OT (Other) – Any other interesting behaviour

PR (Predation) – Details of any predation event

OT (Other) – Anything not categorised above, e.g. injured animal, another male in troop

TE (Technical problems) – GPS ran out of batteries, lost/found monkeys

In addition to the data above, you will need to mark a waypoint for each *ad libitum* recording. The names that you must use are the codes of the subtype (AG, IE, WE, MA, AG), except when this is OT in which case you must use the code of the type (V, BE, PR, OT). Use PR for predation events. Then, with no space and with 2 digits, write the appropriate number (Ex. PR01 27SEP14 B, IE01 04SEP14 B).This is the name that you must write into the **'GPS ID'** column of the spreadsheet.

Downloading data

At the end of each follow day you will need to download your data from both the PDA and the GPS onto the Primate hard drive.